Spatial analysis of anthropogenic disturbance regimes and roadside shrubs in a fragmented agricultural landscape

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Abstract. In fragmented woodlands in agricultural regions of Australia, roadside environments (road verges) provide important refuges for threatened native fauna and isolated populations of plant species. However, as roads are transport corridors for humans and their vehicles, species survival is affected through destruction, fragmentation and modification of remaining habitat by human activity. Few studies have recognised the effects of anthropogenic disturbances, in the form of historical roadworks activities, on adjacent roadside plant populations. The aim of this study was to investigate the effects of soil disturbance from roadworks on the spatial patterns and structural dynamics of roadside *Acacia* populations in an agricultural area in southeastern Australia. Stem size and disturbance data were collected from 135 roadside populations of three species of *Acacia* shrubs in the Lockhart Shire area. Spatial pattern analysis using the Network K-function and Discriminant Function analyses showed that road verge width, road category, disturbance intensity and distance to nearest town were highly significant variables in relation to disturbance from roadworks and shrub structural dynamics. Colonising populations were more abundant along gravel roads where soil disturbance intensity was high, whereas stable populations were more abundant where soil disturbance intensity was low. Senescent populations were more abundant in narrow, little used road verge corridors 4-6 km from nearby towns. These results suggest that anthropogenic disturbance regimes may be critical to shrub recruitment and persistence in roadside environments, which has important consequences for conservation of threatened native flora and fauna in agricultural landscapes.

Keywords: *Acacia*; Discriminant function analysis; Field margins; Fragmentation; Historic ecology; Network K-function; Population structure; Road verge; Soil disturbance.

Nomenclature: Harden (1991).

Abbreviation: CSR = Complete spatial randomness.

Introduction

Spatial heterogeneity at various scales has long been recognised as being important in understanding underlying ecological processes (Watt 1947; van der Maarel 1996). Across a given landscape, populations are not usually distributed uniformly or randomly, but spatial heterogeneity exists, where populations are clustered or form gradients according to an environmental variable or generating process (Turner 1989; Legendre & Fortin 1989; de Blois et al. 2002). Understanding scale dependencies in landscape patterns and processes is critical (Turner 1989; Levin 1992), as various studies have shown the importance of both regional and local scale processes in determining population dynamics (e.g. Ohmann & Spies 1998; Wiegand et al. 1998; Rogers & Hartnett 2001). Rather than trying to choose the correct scale for studies, it is important to understand how landscape pattern and underlying processes change across scales (Levin 1992). Spatially explicit analysis of landscape pattern at various scales can provide revealing insights into underlying disturbance regimes (Niklasson & Granström 2000).

The importance of disturbance processes in shaping the spatial structure and temporal dynamics of ecological systems has been discussed in many reviews (e.g. White & Pickett 1985; Hobbs 1987). Natural and anthropogenic disturbance processes generate patchiness in nature across a wide range of spatial and temporal scales, by altering resource availability and competitive interactions between plant populations (Wiegand et al. 1997; Gómez Sal et al. 1999). Effects of natural and anthropogenic disturbances on plant populations also depend on complex interactions between the life history attributes of individual species, and the spatial and temporal structure of the prevailing disturbance regime (Lovell & Lovell 1985; Clarke 1991a; McIntyre et al. 1995; Yorks et al. 1997). Whilst the spatial pattern of natural disturbances is strongly influenced by landscape heterogeneity of environmental factors, anthropogenic disturbances are often highly selective and spatially arrayed in a logical way (de Blois et al. 2002).

In many fragmented agricultural areas in southeast Australia, roadside environments are often the last refuges for many *Eucalyptus* woodlands and shrubs such as *Acacia* species, which provide vital habitat for threat-

ened fauna (Arnold & Weeldenburg 1990; Bennett 1991). Spatial analysis of roadside shrub populations can reveal important insights into population structural dynamics, stand history and anthropogenic interrelations; issues critical to conservation planning (Motzkin et al. 1996). The purpose of this paper is to investigate anthropogenic disturbances, in the form soil disturbance from roadworks activities, and the distribution and structural dynamics of roadside *Acacia* populations at varying spatial scales. This paper continues from previous studies which have described the effects of soil disturbance from roadworks on adjacent shrub populations (Spooner et al. 2004), and the spatial patterns of roadside *Acacia* species (Spooner et al. in press). In this paper, we examine the spatial pattern of structural groups of *Acacia* populations to investigate which variables are important in predicting anthropogenic disturbance processes, and at what scales.

Methods

Study area

The study was conducted in the Lockhart Shire, southern NSW, Australia (35° 07' S, 146° 26' E), a rural local government area of 365 km² (Fig. 1). The area contains a road network of over 1600 km, consisting of 450 km of bitumen sealed roads, 750 km of constructed gravel roads and 380 km of graded earth and vehicular tracks. The area has a cool temperate climate, with mean annual rainfall ranging from 450 mm in the west to 600 mm in the east. As has occurred throughout the wheat-sheep belt of SE Australia, agricultural development has resulted in the clearing of over 85% of native vegetation, and most patches of intact native vegetation occur along roadsides. Native vegetation consists of open *Eucalyptus* woodlands (e.g. *Eucalyptus microcarpa, E. melliodora,*

E. blakelyi and *E. albens*), as well as mixed *Eucalyptus* (*Callitris glaucophylla* or *Allocasuarina leuhmannii*) communities. Three *Acacia* species are dominant shrubs in remnant vegetation in the area: *Acacia pycnantha,* an obligate seeder, and *A. montana* and *A. decora,* facultative seeders (Bull 1997).

Population sampling and anthropogenic disturbance regimes

In total 135 *Acacia* populations (47 *A. pycnantha*, 48 *A. montana* and 40 *A. decora*) were selected from existing roadside survey data (Bull 1997) using a stratified random sampling procedure (Spooner et al. 2004), and stem size, road and disturbance data were collected (Fig. 1). A population was defined as a minimum of ten individuals, isolated by at least 250 m from other populations of the same species. Previous studies (Spooner et al. in press) used multivariate clustering techniques to classify groups of *Acacia* populations with similar structural characteristics, based on stem sizes of plants in each population. Despite different life-history attributes, population structures for all three *Acacia* species were similar and were classified as 'colonising', 'stable' or 'senescent'. A dendro-ecological study established that *Acacia* stem diameter was correlated with shrub age. Previous studies also revealed evidence of soil disturbance from previous road construction or maintenance activities in over 90% of *Acacia* populations, and a significant relationship between major recruitment pulses in combined *Acacia* populations and road construction events. Road verge width was also found to influence the scale of disturbance effects on population structures. Further details of these analyses are described in Spooner et al. (2004).

Spatial pattern analyses

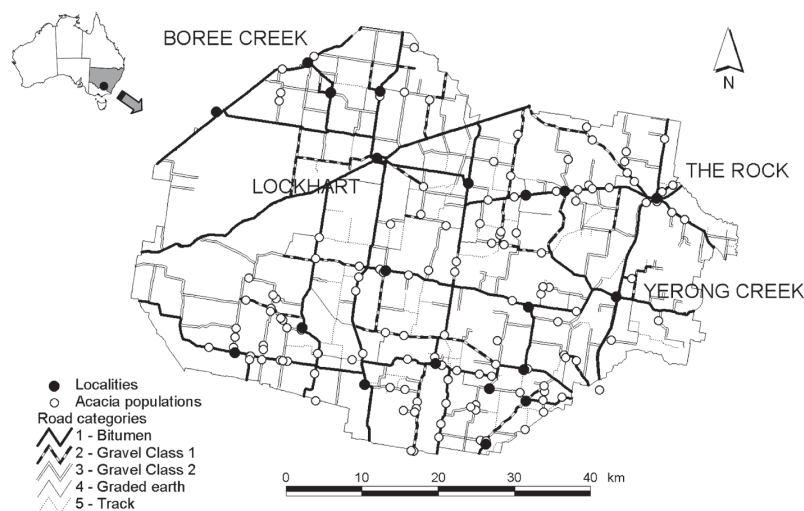To visually inspect spatial patterns of roadside combined *Acacia* populations in the study area, a Kernel

Fig. 1. Location of the study area in southern NSW, Australia, showing the location of 135 populations of *Acacia* species, human localities and road categories.

BOREE CREEK

THE ROCK

LOCKHART

YERONG CREEK

N

● Localities
○ Acacia populations
Road categories
1 - Bitumen
2 - Gravel Class 1
3 - Gravel Class 2
4 - Graded earth
5 - Track

0   10   20   30   40 km

estimation of the density of *Acacia* populations was constructed, using the Animal Movement Analysis GIS extension on Esri Arcview (Hooge 2002). The Kernel process constructs a set of probability polygons that represents a histogram of the intensity of the spatial point pattern of *Acacia* populations (Bailey & Gatrell 1995). This process obtains a smooth estimate of a univariate probability density from the observed cases (in this case, *Acacia* populations), using the least-squares cross-validation technique for the smoothing parameter, and a selected bandwidth of 4 km.

Spatial locations of the three structural groups of combined *Acacia* populations were statistically analysed using the network K-function (Okabe & Yamada 2001; Spooner et al. ln press), a network based development of Ripley's *K*-function (Ripley 1976, 1981; Haase 1995). The network *K*-function detects spatial clustering by calculating the number of points (in this case populations) *P* within the shortest network distance *t* to all other points $P = \{p_1, \dots p_n\}$, which follow a binomial distribution on a finite connected network. The assumption of the binomial point process is based on the hypothesis that points *P* are uniformly and independently distributed over a finite network. Thus if this hypothesis is rejected, points *P* are spatially interacting and may form non-uniform patterns.

The observed univariate network *K*-function, $\hat{K}(t)$ is given by the equation:

$$\frac{|L_T|}{n(n-1)} \sum_{i=1}^{n} \left(\text{the number of points of } P \text{ on } L_{p_i}(t) \right) \qquad (1)$$

where network links (in this case, road lengths between each node) are defined as L_T, and the total network distance as $|Lr|$, and n = number of points. In this case, L_T is the set of road network links in the Lockhart shire council area. Monte Carlo simulations (100) were used to construct a confidence interval envelope based on the

maximum and minimum values from an equivalent number of random co-ordinates for $K(t)$, and plots of $\hat{K}(t)$ were then compared with this envelope to assess significance of departure from complete spatial randomness (CSR) (Diggle 1983). If plots of $\hat{k}(t) > K(t)$ and lie outside the upper confidence interval, then points *P* tend to be clustering. Conversely, if plots of $\hat{k}(t) < K(t)$ and lie outside the lower confidence interval, then points are tending towards regularity (Bailey & Gatrell 1995).

For bivariate network cross *K*-function analyses, two kinds of points,

$$A = \{a_1, \dots, a_n\} \text{ and } B = \{b_1, \dots, b_n\}$$

were analysed on L_T, where the number of points A are calculated within a network distance *t* of points *B*. In this case, spatial locations of different structural groupings of *Acacia* populations were compared to locations of human localities (towns). The observed bivariate network cross *K*-function is given by the equation:

$$\hat{K}^{ba}(t) = \frac{|L_T|}{n_a n_b} \sum_{i=1}^{n_b} \left((\text{the number of points of } A \text{ on } L_{b_i}(t)) \right) \quad (2)$$

If $\hat{K}^{ba} > K^{ba}(t)$, then points *A* tend to be clustered around points *B*. If $\hat{K}^{ba} < K^{ba}(t)$, then points *A* tend to be repelling away from points *B*. Statistical tests are similar to the univariate network *K*-function $K(t)$, where the spatial scale at which the two groups 'attract' or repel' is determined. Spatial point patterns of the three structural groups of *Acacia* species were analysed on a road network shape-file using SANET Version 1.0 – 021125 on ESRI Arcmap (Okabe et al. 2002). Output data from SANET was exported into MS Excel to aggregate data and produce graphs for analyses. For network bivariate analyses, the present version of SANET does not provide a means to test significance of departure from null interaction (Bailey & Gatrell 1995; Okabe & Yamada 2001). To check for statistical significance of departures

Table 1. Description of 12 scale-dependent disturbance and environmental variables used in discriminant function analyses.

Landscape scale		
1	Distance to nearest locality	Km
2	Shrub kernel	Location in kernel distribution (0–90% percentile bands) for all *Acacia* spp.
3	Species	1 = *A. pycnantha*; 2 = *A. montana;* 3 = *A. decora*
4	Road category	1 = Bitumen; 2 = Gravel (Class 1 and 2); 3 = Earth formation; 4 = Track
Road verge scale		
5	Road verge width	0 – 90 m; for side of road where population was situated
6	Total corridor width	0 – 100 m
7	Traffic thoroughfare	1 = No through road, 2 = normal, 3 = intersection or line-of-sight
Patch scale		
8	Population area	Variable
9	Drainage	1 = Run-off; 2 = Run-On; 3 = Ditch
10	Soil disturbance intensity	0 = nil, 1 = grading (up to 0.1 m deep); 2 = drains or gutters (up to 0.5 m deep); 3 = soil extraction (> 0.5 m deep), or major earthworks (cut or fill).
11	Topography	1 = crest; 2 = upper slope; 3 = mid-slope; 4 = lower slope; 5 = flat; 6 = floodplain
12	Tree cover	0 – 100% overstorey cover

Table 2. Discriminant function analyses Wilk's λ-test, associated P-value, and classification statistics for individual and combined landscape, road verge and patch scale predictor variables. * = significance ($P < 0.01$); † = variables included in final model (L × R × P).

No.	Predictor variable		Wilk's λ-test		Classification success (%)			
			λ	P	1	2	3	Total
	Landscape scale (L)							
1 †	Distance to nearest town							
2 †	Shrub Kernel							
3	Species							
4 †	Road category	L	11.454	0.177	12.5	38.6	79.2	47.6
	Road verge scale (R)							
5 †	Road verge width							
6	Corridor width							
7	Traffic	R	12.892	0.012	31.3	26.1	77.6	47.2
		L × R	22.745	0.012	31.3	27.3	77.1	47.6
	Patch scale (P)							
8	Area							
9	Drainage							
10 †	Disturbance intensity							
11	Topography							
12	Tree cover	P	11.092	0.026	28.1	34.1	79.2	50.0
		L × R × P	**31.539**	**< 0.001 ***	**46.9**	**43.2**	**79.2**	**58.1**

of $\hat{K}^{ba}$ from $K^{ba}(t)$, an approximation of the 95% confidence envelope was constructed by calculating the standard deviation (s.d.), and values of ±1.96 * s.d. were accepted for maximum and minimum intervals.

Discriminant function variables

Landscape, road verge and patch scale variables were selected for discriminant analysis based on their likely relationships with anthropogenic disturbances on roadside *Acacia* populations (Table 1).

Landscape scale variables.

The spatial patterns of *Acacia* populations (Fig. 1), and the historical development of roads in the study area (Prichard 1991) indicated a possible spatial relationship between shrub populations and human towns (Variable 1; Tables 1 and 2). A Kernel estimation (see above) of combined *Acacia* populations (V2) was used to differentiate habitat preferences of *Acacia* species from disturbance effects and individual species responses (V3). Different categories of roads receive different levels of funding from external government agencies. For example, a Category 1 road receives 100% external funding, a Category 2 road is funded in a 60/40 agreement, a Category 3 road 40/60 etc. Therefore road category may result in different management inputs to roads and adjacent *Acacia* populations (V4).

Road verge scale variables.

Previous studies have shown that road verge width (V5) influences the scale of disturbance effects in *Acacia* populations (Spooner et al. 2004). Populations situated in narrow verges are more likely to be impacted on by road disturbances. As the placement of the road surface varies within the road corridor reserve, and historic

development of roads often causes patchy disturbances within road reserves, total corridor width (V6) was also entered. Traffic thoroughfare (V7) is a variable to account for varying levels of road maintenance to remove vegetation for road safety reasons, with Category 1 (no through roads) receiving low inputs and Category 3 (intersection or line-of-sight) receiving high inputs.

Patch scale variables.

Population area (V8) was entered, as shrub populations that cover a larger area may have an increased chance of disturbance from road construction and maintenance. Drainage (V9) of the site adjacent to the road surface may also affect ongoing impacts from road maintenance. Where soil disturbance has occurred in a population, the degree of soil disturbance intensity (V10) is important as, in conjunction with plant life-history attributes, this dictates the rate of recovery of patch and future regeneration prospects. The topography (V11) of a patch may also influence soil disturbance intensity; e.g. a population of shrubs on hilly areas may have high disturbance inputs from road construction necessary for cut and fill operations, whereas populations in flatter areas may have fewer disturbance inputs. As large mature trees can inhibit road machinery, tree cover (V12) was entered as a disturbance variable, on the premise that greater overstorey tree cover would result in less soil disturbance in associated *Acacia* populations.

Discriminant function analysis

Discriminant function analysis was used to build a predictive model of group membership based on disturbance variables for each population, using SPSS Version 10.0.7. This method generates a set of discrimi-

nant functions based on linear combinations of the predictor variables that provide the best discrimination, or mean difference, between pre-assigned groupings of age structures (Huberty 1994). Data for each *Acacia* species were pooled to build a predictive model that explained spatial patterns of combined *Acacia* populations previously classified as either 'colonising' (Group 1; $n = 40$), 'stable' (Group 2; $n = 48$) or 'senescent' (Group 3; $n = 49$) (Spooner et al. 2004).

Predictor variables were checked for normality via visual inspection of probability plots, however non-normality of some predictor variables was accepted, leading to reduced predictive power rather than increased Type 1 error (Huberty 1994; Anon. 2002). However, as discriminant analyses are highly sensitive to outliers, exploratory analyses were performed and scatter-plots visually inspected to identify outliers. This process identified four sites with a patch width > 90 m, which adjoined a remnant patch of vegetation and had no 'formal' road corridor boundary. These sites were excluded from subsequent analyses.

Discriminant function analyses were performed using a stepwise entry, with tolerances of $F = 1.2$ for entry and $F = 1.0$ for removal, where all predictors are entered, and those variables with the smallest partial correlation which contributed least to the discriminant functions systematically eliminated. This method was performed for landscape, road verge and patch scale variables separately, and then for all variables combined to investigate multiple scale effects. To interpret discriminant functions, Wilk's λ-test was used to show the level of significance for each of the discriminant functions, with associated χ^2 and *P*-statistics calculated This is a measure of the differences among group means on the independent variable. Standardized β-coefficients (canonical discriminant function coefficients) were examined to determine the contri-

bution, or weighting, of each variable to the discrimination between groups. Function values at group centroids and differences between group means for significant variables were also examined to interpret discriminant analysis results. Classification statistics were tabulated to show predicted group membership and the degree of success of the model (Huberty 1994; Anon 2002).

Results

A Kernel estimation of the density of combined roadside *Acacia* populations in the landscape identified four strong clusters of populations within 50% probability polygons. From visual inspection, spatial point patterns appeared to be non-random and the centroids of many clusters were located near human townships or localities (Fig. 2). Univariate network *K*-function analysis of structural groupings of combined *Acacia* populations showed varying results at different scales. At large scales $(t > 12$ km$)$, plots of $\hat{K}(t)$ vs *t* showed that *Acacia* populations were randomly distributed across the study area for all three age structural groups (colonising, stable and senescent). However, at small scales (Fig. 3), plots of $\hat{K}(t)$ vs *t* showed a general trend across age structural groups, from colonising populations that were randomly distributed (Group 1: Fig. 3a), to stable populations tending to cluster at distances < 6 km (Group 2: Fig 3b), to senescent populations that were significantly clustered at distances < 6 km (Group 3: Fig. 3c).

Bivariate spatial pattern analysis using the Network cross *K*-function was used to investigate the spatial interaction between *Acacia* populations and human localities, as observed in Kernel analysis. Plots of $\hat{K}^{ba}$ vs $K^{ba}(t)$ showed no significant spatial interaction between 'colonising' (Group 1) or 'stable' (Group 2) populations

Fig. 2. Kernel estimation of the spatial point density of combined *Acacia* populations on the road network, with Group 1 (colonising), Group 2 (stable) and Group 3 (senescent) populations shown (localities and roads omitted for clarity).
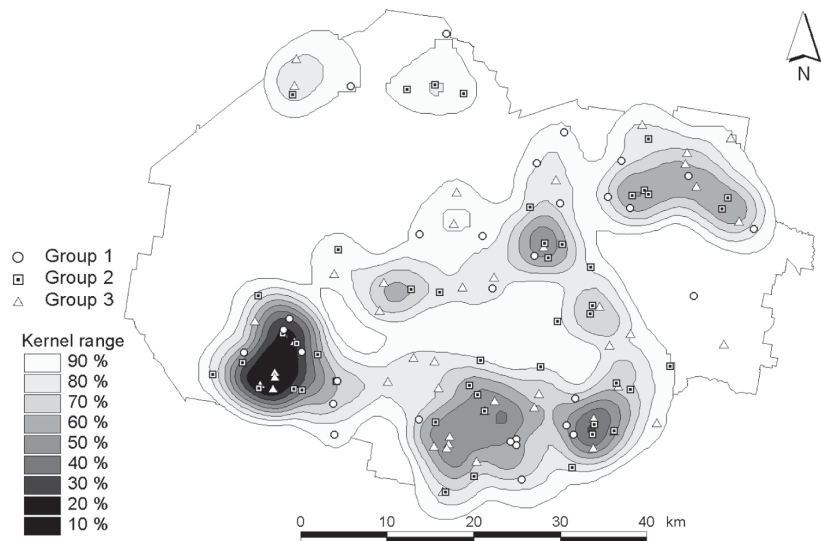
and adjacent towns on the road network (Fig. 4). In contrast, plots showed significant 'attraction' between the spatial distribution of 'senescent' populations (Group 3) and neighbouring human towns at large scales ($t > 30$ km). In conjunction with the univariate K-function analysis of senescent populations (Fig. 3c), these results show that there was significant clustering of senescent populations at small scales (4-6 km distance), and there was significant spatial attraction between clusters of senescent populations and nearby towns when examined at large scales (> 30 km).

Spatial data were used to determine significant variables associated with underlying anthropogenic disturbance processes. Discriminant function analysis produced a useful predictive model that classified 58.1% of *Acacia* population structures successfully, with two functions that combined five patch, road verge and landscape scale variables (Table 2). For this final model, discrimination between groups of shrub populations was significant ($\lambda^2 = 31.5$, $P < 0.001$), and 46.9% of colonising, 43.2% of stable and 79.2% of senescent populations were classified successfully (Table 2). In order of importance, road verge width (Variable 5), disturbance intensity (V10) and road category (V4) had the greatest contribution to Function 1 in the final discriminant model, whereas distance to nearest locality (V1) and shrub kernel (V2) had the greatest contribution to Function 2 (Table 3). Function 1 variables (road verge width, disturbance intensity and road category) accounted for 83.4% of group variance in the final discriminant model, which indicated that Function 2 variables of distance to nearest town (V1) and preferred shrub habitat (V2) provided only a small refinement to the overall model. Landscape, road verge and patch scale variables were also analysed in separate discriminant analyses, but results were non-significant.

Differences between group means for significant variables (Table 4) were then used to interpret the final discriminant model and Network *K*-function results. In general, colonising populations were more abundant along gravel roads in wide road verges where soil disturbance intensity was high (e.g. cut or fill operations). Stable populations were also more abundant in wide road verges,

Table 3. Standardized discriminant function coefficients (β) for significant predictor variables in final discriminant model (largest contribution between each variable to any function shown in bold).

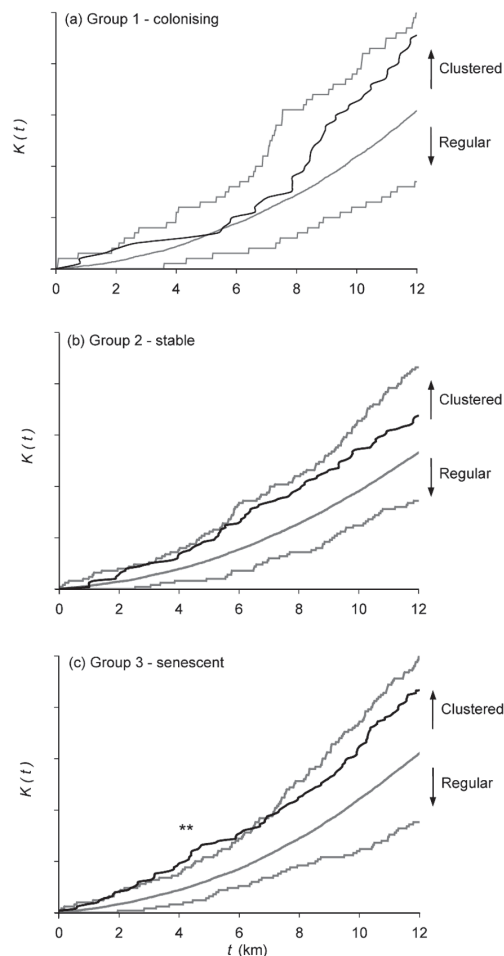| No.	Predictor variable	Function 1	Function 2
1	Distance to nearest town	− 0.054	**0.895**
2	Shrub Kernel	0.108	**− 0.605**
4	Road category	**0.605**	0.119
5	Road verge width	**0.910**	0.017
10	Disturbance intensity	**0.767**	0.358

Fig. 3. Univariate network *K*-function analysis of *Acacia* age structural groups **(a-c)** at 0-12 km scale, showing the observed statistic $\hat{K}(t)$ (black lines) plotted against t for the Lockhart study area. The grey lines give the 95% confidence interval and mean value for CSR (central grey line), ** indicates a significant result.

but in contrast to colonising populations, where more abundant where soil disturbance intensity was low, in areas of slightly less preferred habitat. Senescent populations were spatially correlated and more abundant in narrow road verge corridors at a distance of 4-6 km from nearby towns, often in little used access roads or lanes, in slightly more preferred habitat (Table 4).

Discussion

A major goal of plant ecology is to determine the factors that control species distributions and community composition within a landscape (Motzkin et al. 1999). To do this, suitable statistical analysis techniques are required to determine whether spatial point patterns for individual species are random, clumped or regular
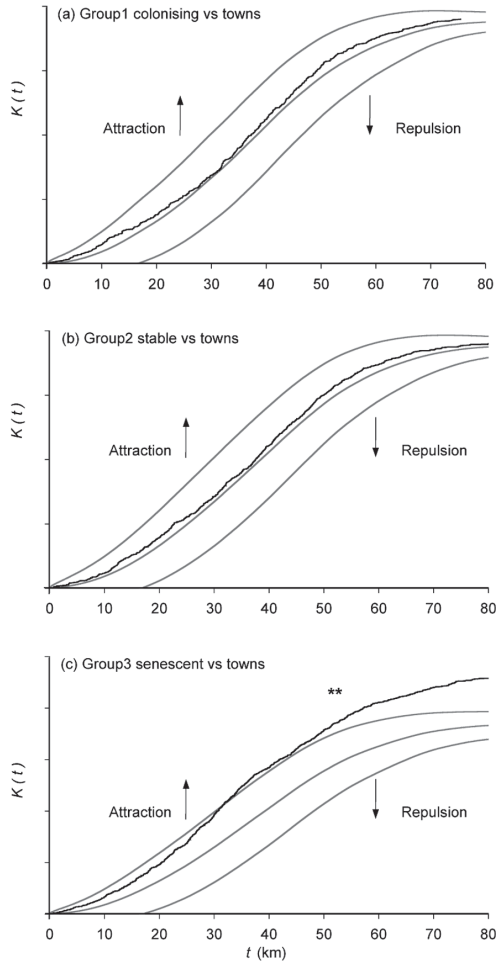
Fig. 4. Bivariate network *K*-function analysis of *Acacia* structural groups versus towns (**a-c**), showing the observed statistic $\hat{K}(t)$ (black lines) plotted against *t* for the Lockhart study area. The grey lines give the 95% confidence interval and mean value for CSR (central grey line); ** = significant result.

Table 4. Group means for significant predictor variables in final discriminant model. Values in bold indicate group separation, based on information from structure matrix and group centroids.

No.	Predictor variable	Group 1 colonizing	Group 2 stable	Group 3 senescent
1	Distance to nearest town (km)	4.2	4.1	**5.1**
2	Shrub Kernel (%)	46.5	**48.8**	45.1
4	Road category (1-4)	**2.3**	2.0	2.1
5	Road verge width (m)	45.4	45.1	**38.0**
10	Disturbance intensity (1-3)	**1.9**	1.4	1.5

lations were more randomly distributed. This result was unexpected, demonstrating the importance of using appropriate statistical analysis techniques in network applications. Bivariate Network cross K-function analyses showed that although clusters of senescent populations were located away from towns, there was strong spatial interaction with human towns or localities at large scales. This clustered pattern of older, senescent populations, compared to colonising populations which were more randomly distributed, was highly unusual. Since previous studies have described the effects of soil disturbance from roadworks on *Acacia* shrub populations (Farrell & Ashton 1978; Spooner et al. 2004), these results suggest a strong influence from anthropogenic disturbance processes on the maintenance of *Acacia* populations.

Understanding spatial patterns of roadside shrubs

Although important spatial patterns were detected using Network K-function analyses, further discriminant function analyses revealed the highly complex nature of underlying disturbance processes. Road verge width was the most important variable in predicting shrub population structures, followed by disturbance intensity from roadworks and road category. Road verge width is likely to govern the size and shape of disturbance from roadworks, and road category influences the frequency at which roadworks occur (see Methods). Therefore these results suggest that the size, shape, intensity and rate of anthropogenic disturbances are important in determining the age distribution of roadside *Acacia* populations, which has important implications regarding their overall persistence in the landscape.

Moloney & Levin (1996) proposed a three level organisational scheme to model the spatial and temporal structure of a disturbance regime, based on (1) overall rate and intensity of disturbance, (2) size and shape of the disturbance and (3) the spatial and temporal structure of the disturbance regime. The results of our analysis confirm the usefulness of this framework in modelling the impacts of disturbance from roadworks in a heterogeneous road network on shrub populations. Essentially, each road has its own unique combination of properties (e.g.

(Jeltsch et al. 1999). Clumping or regular patterns are often interpreted in terms of patchy availability of resources, competition, stability and regeneration or disturbance ecology (e.g. Harper 1977; Legendre & Fortin 1989; White & Pickett 1985; Clarke 1991b). Irregular patterns are of particular interest, as these may sometimes reveal human driven disturbance processes that overrule natural dynamics (de Blois et al. 2002).

The results of our study showed that colonising, stable and senescent population structures of combined *Acacia* species had different spatial distributions on roads in the study area. Initial visual inspections of spatial distributions using Kernel analysis appeared to show strong clustering of shrubs across the landscape. However, univariate network K-function analysis of individual population structural groups showed that 'senescent' populations were significantly clustered, 'stable' populations tended to cluster and 'colonising' popu-

width, category and development history), therefore disturbance impacts from roadworks are road specific and vary over time, which explains much of the complex nature of the spatial patterns of shrub populations observed.

In terms of the broader spatial and temporal structure of the disturbance regime, discriminant function analysis also showed that landscape scale variables exerted a more subtle influence on shrub structural dynamics than patch or road verge scale variables. The spatial association between human towns and senescent population structures demonstrates the importance in understanding human logic regarding roadworks activities (Baker 1999). For example, roads have progressively developed from the centre of townships in the study area, generally resulting in a greater frequency of disturbances closer to towns and less inputs away from towns (Prichard 1991). A possible explanation for senescent shrub populations being located further away from human towns, but spatially interacting, is that the size, intensity or frequency of disturbance from current roadworks in these areas is insufficient for on going recruitment from older plants. No species differences were detected in response to roadworks, however the preferred habitat of combined *Acacia* populations (shrub kernel) was a significant environmental variable, revealing natural vegetation patterns in roadside environments that underlie more recent impacts of disturbance from roadworks (McIntyre & Lavorel 1994; Ullman et al. 1995).

Discriminant analyses also showed that, taken individually, predetermined patch, road verge or landscape scale variables were not adequate to describe the effects of anthropogenic disturbance on roadside shrub populations but instead, a combination of varying scale variables provided a more robust model. These results highlight how anthropogenic disturbance processes provide an ecological connection across scales, affecting population structures and patterns across a given landscape, depending on plant life-history attributes (Clarke 1991a; Peterson et al. 1998). Similar to a fire regime, soil disturbance from roadworks at small scales creates a homogeneous environment, by removing the aboveground biomass and producing areas of even aged vegetation. But at larger scales, soil disturbance from roadworks produces heterogeneity, by creating a complicated historical mosaic of disturbed and undisturbed roadside environments (Motzkin 1996; Peterson 2002).

Though a significant model was obtained from discriminant analyses, correlations between the selected variables and population structural groupings were not ideal, indicating that other disturbance or environmental variables may also influence the population dynamics of roadside shrubs. As road width was a significant variable affecting the size and shape of disturbances from

roadworks, spatial data about the position of shrub stands relative to the roadway edge, rather than population area (as used in this study) may lead to greater predictive power of disturbance impacts. For example, senescent populations were often located in narrow road corridors, with mature shrubs surviving along fence lines. More fine-scale detail could be incorporated into the model, such as adjacency of shrubs stands to farm entrances, as these areas appear to be subjected to a higher rate of roadworks inputs (P. Spooner pers. obs.). Incorporation of further historical data relating to road development, such as road reserve allocation and construction dates, in conjunction with maintenance records would also be highly useful.

Anthropogenic disturbance regimes

Disturbance is a discrete event that modifies a landscape, ecosystem, community or population structure, which can reduce plant biomass by causing its partial or complete destruction, and provide a diverse set of new conditions for seedling establishment and plant growth (Harper 1977; Grime 1979; White & Pickett 1985). For fire-adapted woody shrubs such as *Acacia* (Gill 1981), soil disturbance of a soil seed bank by roadworks assists establishment by breaking seed dormancy and providing an ideal substrate for establishment (Abrahamson 1980; Mott & Groves 1981). Mechanical removal of the aboveground organs from roadworks activities can also promote vegetative resprouting in some species (e.g. *A. decora*). As fire was absent in all but two sites, soil disturbance from past road construction appears to explain much of the pulsed recruitment in roadside *Acacia* populations (Spooner et al. 2004). We hypothesise that, for *Acacia* species, soil disturbance from roadworks acts as a surrogate disturbance agent for small-scale natural soil disturbances and fire, which is now mitigated in most agricultural areas (Hobbs 1987; Benson 1991). Colonisation and stability of populations depends on the timing of soil disturbances from roadworks in relation to a plant's reproductive biology (Clarke 1991a, b).

The effects of disturbance on plant population dynamics have been the topic of many conceptual and empirical studies (e.g. Grime 1979; Noble & Slater 1980; White & Pickett 1985; Clarke 1991b; Levin 1992). Dominant themes are the spatial and temporal aspects of disturbance in relation to population structural dynamics. Much of the spatial and temporal variability in roadworks activities can be attributed to historical changes in road use and management (Bennett 1991). For example, increases in more intensive farming practices have resulted in increased transportation of inputs (e.g. fertilizers, pesticides) and higher volumes of crops transported for processing. Growth in human settle-

ments exerts changing demands on local municipalities responsible for road maintenance. However, narrow winding roads originally surveyed for farm access were not designed for car or heavy transport traffic (Prichard 1991; Pauwels & Gulinck 2000). Consequently, as road use changes over time, roads are often re-aligned, re-surfaced or widened, and as usage dictates, improved with cuttings drainage or embankments, directly affect-inß adjacent environments (Way 1977; Anderson 1994). This variability in road management history affects shrub dynamics, as the energy required to construct and maintain roads is often transferred into the surrounding roadside environment, resulting in pulsed recruitment from infrequent, but to some extent predictable, disturbance events (Bennett 1991; Naveh 1998).

From the spatial patterns we have identified, we hypothesise that anthropogenic disturbance regimes are a critical process affecting *Acacia* population dynamics in roadside environments such as those in southeastern Australia. By developing an explicit understanding of the spatial and temporal architecture of the disturbance regime, predictions can be made of the level of impacts of disturbance on plant populations, based on a set of simple variables (Turner 1989; Moloney & Levin 1996). These results have highlighted the uniqueness of a range of roadside environments owing to individual anthropogenic disturbance regimes. As such, this 'cultural vegetation' relies on human relationships for continuing existence (Kirkpatrick 1999). Acknowledgement of human activities in the development of roadside ecosystems is important for conservation, as current efforts towards complete 'protection' could potentially lead to the impoverishment of structural and biological diversity (Naveh 1998). Unfortunately, present conservation biology research tends to concentrate on relatively pristine areas with high species biodiversity, or ignores human impacts due to lack of understanding or complexity (Foster 2000; Miller & Hobbs 2002). A more dynamic perspective of roadside ecosystems (and other remnant vegetation), which includes consideration of anthropogenic impacts, is essential in decisions about the management of biodiversity in cleared and fragmented agricultural landscapes.

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