

# Evidence for the Spatial Self-organisation of Litter Patches in a Semi-arid Woodland

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## ABSTRACT

Spatial self-organisation of plants and soils is a typical feature of many systems. Different mechanisms have been proposed to explain self-organised patterns, including scale-dependent feedbacks and disturbance recovery mechanisms. In semi-arid systems, there is limited evidence for the spatial self-organisation of leaf litter despite its obvious presence within self-organised vegetation patches. Here we provide field-based evidence for the spatial self-organisation of surface litter. We measured the cover, size distribution and spatial arrangement of perennial vegetation patches and surface litter patches in four vegetation communities in a semi-arid woodland, one of which had been cleared of trees 50 years previously. The effects of tree removal were still evident 50 years after clearing, with greater perennial patch cover and greater variability in surface litter arrangement in the

cleared community than the uncleared analogue. Across all communities, we detected a high correlation between perennial patch cover and litter cover. We found no evidence to support scale-dependent feedbacks occurring between litter and perennial patches, with little relationship between perennial patch size and the strength of its association with litter. The distribution of litter patch sizes was consistent with a truncated power law relationship, suggesting that disturbance–recovery mechanisms may play an important role in the spatial self-organisation of litter, particularly through large-scale processes such as wind disturbance.

**Key words:** Litter dynamics; Mallee; Self-organisation; Patch dynamics; Truncated power law; Shrubland.

## INTRODUCTION

The development of resource patches is a fundamental process in resource-limited environments

and is critically important for the maintenance of ecosystem functions (Ludwig and Tongway 1995). In arid and semi-arid ecosystems resource patches are associated with perennial features of the landscape, typically perennial vegetation and related components. The perennial plants themselves, as well as stumps, logs and surface litter, engineer the landscape by concentrating essential resources (soil, water, nutrients, leaf litter) into discrete zones (that is, resource-rich patches, fertile patches, resource islands). These patches provide resources for patch-dependent taxa (Shachak and others 2008; Badano and Cavieres 2006) and increase the effi-

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ciency with which resources are allocated and used (Ludwig and Tongway 1995; Rietkerk and others 2011). Leaf litter is an important ecosystem component and resource, providing fuel for fires; a source of carbon, nitrogen and other trace elements; and a substrate for feeding, breeding and sheltering habitat for a variety of arthropods, reptiles, mammals and birds (Haslem and others 2011). Despite considerable research covering the importance of such patches, there have been relatively few attempts to explain how they develop. One proposed mechanism for patch development is spatial self-organisation (Kefi and others 2007; Rietkerk and Van de Koppel 2008).

Spatial self-organisation is a phenomenon whereby initially disordered conditions are transformed into large-scale patterns through smaller-scale, dissipative interactions among organisms and their environment (Kessler and Werner 2003; Rietkerk and Van de Koppel 2008). Spatial organisation is characterised by a wide range of large-scale, regular and irregular patterns, forming shapes such as spots, stripes and rings (Ludwig and others 1999; Tongway and others 2001; Kessler and Werner 2003), which can be important drivers of ecological diversity, stability and resilience (Pascual and Guichard 2005; Rietkerk and Van de Koppel 2008). Regular and irregular patterns have been observed in intertidal mussel beds (Guichard and others 2003), fire-prone forests (Malamud and others 1998), polar and high alpine stone and soil arrangement (Kessler and Werner 2003), savanna (Lejeune and others 2002) and semi-arid vegetation cover (Kefi and others 2007). Understanding the mechanisms that contribute to spatial self-organisation is a critical component of managing self-organised systems.

The spatial self-organisation of vegetation in arid and semi-arid ecosystems has been explained by a number of mechanisms including scale-dependent feedbacks (Rietkerk and Van de Koppel 2008) and disturbance–recovery mechanisms (Pascual and Guichard 2005). Scale-dependent feedbacks involve feedbacks between an organism and its environment, which switches from being positive at small scales to negative at larger scales (Rietkerk and Van de Koppel 2008). In arid systems, scale-dependent feedbacks associated with water availability may drive patterns in perennial vegetation arrangement, whereby small-scale facilitation at the patch scale (positive feedback) occurs concurrently with broader-scale competition for water (negative feedback) (Klausmeier 1999; HilleRisLambers and others 2001). In contrast, disturbance–recovery mechanisms can be applied at any level of

organisation, spatial or temporal, as an adaptive feature of an ecosystem in response to cycles of disturbance and recovery (Pascual and Guichard 2005). These mechanisms involve a large-scale disturbance prompting small-scale interactions to promote recovery. Disturbance–recovery mechanisms may also describe how perennial vegetation functions and self-organises in arid and semi-arid ecosystems (Rietkerk and Van de Koppel 2008; Kefi and others 2011).

It is likely that the arrangement of vegetation further drives the arrangement of surface litter. In open systems the spatial properties of litter beds appear to be strongly linked to the spatial properties of the canopy from where the material is derived (McElhinny and others 2010; Travers and Eldridge 2012). If litter patch development occurs under local positive interactions, such as local facilitation by perennial vegetation, the patch size distribution of litter should follow a power law (Kefi and others 2007). However, if these local positive interactions were to break down or played a subordinate role, litter patch size distribution may instead follow a truncated power law (Kefi and others 2007). Truncated power law size distributions occur where large, low frequency patch sizes are absent in the landscape. Although leaf litter generally accumulates around the base of perennial vegetation, there is limited empirical evidence for this. There are also few data on the spatial self-organisation of leaf litter, or for the association of litter patches with perennial patches.

This study focuses on field evidence to support the notion that leaf litter self-organises in response to the arrangement of perennial patches. Our study system allowed us to examine perennial vegetation that varies in composition, size and spatial distribution among associated geomorphic surfaces sharing a landscape. We examined the spatial pattern of perennial patches and litter patches in a dune–swale ecosystem, ranging from a community dominated by eucalypt trees lacking a woody understorey, to a more open community of eucalypts with isolated shrubs, to an open woodland with and without a dense shrubby understorey resulting from previous tree removal and soil disturbance. We measured the cover, size distribution, composition and spatial arrangement of perennial patches and patches of surface litter to test the following four hypotheses. At the community scale, we expected that (1) the cover of surface litter patches would increase with increasing cover of perennial vegetation patches. We also expect that (2) the size distribution of perennial patches and litter patches would be similar, despite differences in perennial

patch composition, consistent with either a power law or exponentially truncated power law distribution. This was tested with model fitting and AIC selection. This provides evidence for the occurrence of small-scale processes related to disturbance–recovery mechanisms. Alternatively, if positive feedback processes operate in these systems, then we would expect that (3) as perennial patch size increases, patches become more strongly associated with litter patches (that is, positive feedback). We tested this using Local Indicator of Spatial Association analyses (LISA), predicting that perennial patch size is strongly correlated with the LISA indices. Finally, we used semi-variograms to test whether prior disturbance would influence the spatial arrangement of both perennial patches and litter patches in order to identify potential mechanisms driving the distribution of litter. Specifically, we predicted that (4) the litter arrangement would be most variable, that is, a smaller autocorrelation range, in our disturbed community (Daryanto and others 2013).

## METHODS

### Study Site

Our study was undertaken within the Australian Wildlife Conservancy's Scotia Sanctuary in south-western, New South Wales, Australia (33°43' S, 143°02' E). This area is semi-arid, receiving about 250-mm annual rainfall. Rainfall is highly spatially and temporally variable. Average daily winter (July) temperatures range from a minimum of 6°C to a maximum of 17°C, while summer (January) daily temperatures range from a minimum of 19°C to a maximum of 33°C (BOM 2012). The soils at our site are mainly calcareous, brownish and siliceous sands. Our study was carried out in an area that (1) had not burned in over 50 years; (2) has a short history of light grazing-induced disturbance (Westbrooke 2012); (3) contained small sections that were cleared in the 1960s; (4) is currently free from any disturbance effects created by introduced mammalian herbivores (for example, feral goats) and (5) contains reintroduced soil disturbing mammals including the Greater bilby (*Macrotis lagotis*) and Burrowing bettong (*Bettongia lesueur*). This allowed us to examine the process of litter patch formation and spatial organisation under relatively unmodified (that is, pre-European) as well as modified (that is, cleared) conditions.

Data were collected from four vegetation communities; three were in natural states (that is, un-cleared) and one a modified state (that is, cleared)

with significantly different vegetation composition compared with its naturally timbered analogue. Dune Mallee Woodland (hereafter 'dune') occurs on the sandy dune crests of long, low (relief to 7 m) east–west trending sand dunes. The overstorey vegetation is dominated by eucalypt mallee trees (*Eucalyptus gracilis* F. Muell., *E. dumosa* A. Cunn. ex J. Oxley and *E. socialis* F. Muell. ex Miq.) and the understorey by scattered perennial hummock grasses (*Triodia scariosa* N. T. Burb.). Shrub cover to 2 m is sparse on the dunes (Westbrooke and others 1998). Semi-arid Sand Plain woodlands occurs on soil with alkaline calcareous subsoils, supporting the growth of large (to 8 m tall) *Casuarina pauper* F. Muell. ex L. A. S. Johnson trees, which are the dominant overstorey species (hereafter 'uncleared plain'). Other perennial species dominating this community include *Eremophila sturtii* R. Br., *Senna artemisioides* subsp. *filifolia* (Benth.) Randall and *Dodonaea viscosa* subsp. *angustissima* (L. f.) J. G. West. In some areas of this community large *C. pauper* trees were removed during the 1960s (hereafter 'cleared plain'). The remains of these trees are still visible on the surface where they form large debris piles of coarse woody debris. Sand Plain Mallee Woodland (hereafter 'swale') occurs as a transitional community between the dunes and the plains. The overstorey is dominated by Eucalypt mallee trees (*E. gracilis*, *E. dumosa*, *E. socialis*), whereas the understorey is dominated by the perennial shrubs *Eremophila sturtii*, *S. artemisioides*, *D. viscosa* and *Acacia burkittii* F. Muell. ex Benth. (Westbrooke and others 1998).

### Field Measurements

Data were collected from nine replicate sites in each of the four communities (dune, swale, un-cleared plain, cleared plain) in January 2009 ( $n = 36$  sites). At each site, we established a 50-m-long transect along which we measured, using the line-intercept method (Maestre and Cortina 2004; Kefi and others 2007), the cover of two types of patches; (1) perennial patches associated with tree and shrub canopies and coarse woody debris (logs, stumps and sticks  $>5$  cm across; henceforth 'perennial patches') and (2) surface-resident litter patches (henceforth 'litter patches',  $\geq 2$  cm wide). Patch sizes were estimated to the nearest 1 cm. We also recorded the type of perennial patch, that is, tree, shrub, coarse woody debris (CWD). Where patches overlapped, for example a shrub or log occurred under a tree, both patch types were recorded for our analyses where we required patch types to be distinguished. This allowed us to measure patch length; distance between patches and

provided a 5000-point binary (that is, presence of a patch = 1, absence of a patch = 0) dataset for litter and perennial patches for each transect.

## Analytical Procedures

### Cover of Perennial and Litter Patches

We used linear regression (Minitab 2010) to examine the relationships between the cover of perennial patches and litter patches based on the percentage of the transect that they occupied. As it was possible for multiple patch types to overlap, the sum of each patch type is greater than the overall cover of perennial patches. One-way ANOVA was used to compare, among communities, the number of patches per transect and the percentage cover of each transect that perennial and litter patches occupied. A least significant difference (LSD) test was used as a post hoc test for significant differences. All cover data, except total combined perennial patches, were log<sub>10</sub>-transformed to meet the assumptions of ANOVA.

### Size Distribution of Perennial and Litter Patches

To compare the patch size distribution of perennial and litter patches within and among communities, we modelled the distribution of both litter and perennial patch sizes for each community (Kefi and others 2007). We used a maximum likelihood estimator to estimate the size distribution of patches ( $x$ ). We fitted two distribution models for each patch type in each community: a power law ( $x^2$ ); and a truncated power law with an exponential cut-off ( $x^2 \cdot \exp^{-\beta x}$ ) (Kefi and others 2007; Pueyo 2011). The  $\beta$  parameter in the truncated power law can be used to measure the degree of truncation, indicating the patch size at which truncation occurs (Kefi and others 2007). The model of best fit was selected using AIC. These analyses were run using the ‘fitting’ function in the ‘brainwaver’ package (Archard 2012) in R (R version 3; R Core Team 2013). We plotted patch sizes on cumulative frequency plots to visualise the size distribution of perennial and litter patch sizes summed within each community. To compare potential differences in perennial patch and litter patch sizes within and among each community, we used the Kolmogorov–Smirnov test, ‘ks.test’ function in *stats* package in R (R version 3; R Core Team 2013). To guard against Type I errors, we carried out Bonferroni-adjusted significance tests for pairwise comparisons.

### Spatial Association Between Perennial and Litter Patches

The spatial characteristics of perennial and litter patches were determined with Spatial Association by

Distance Indices (SADIE, Perry 1998; Perry and others 1999). SADIE characterises the spatial properties of count, binary or continuous data, which are not required to meet any particular distribution prior to analysis. This method is based on a ‘distance to regularity’ which is calculated through a randomisation process using the transportation algorithm (Kennington and Helgarson 1980) and at least 780 randomisations. The distance to regularity is the distance that the sampling unit (in this case the presence of a patch) would need to move to achieve an arrangement whereby all sampling units had the same value (that is, all patches were the same size and distance apart) (Maestre 2003). The division of each measured distance by the calculated mean distance gives an index of aggregation ( $I_a$ ), which indicates whether the sampling units are clumped ( $I_a > 1$ ), regular ( $I_a < 1$ ) or randomly ( $I_a \approx 1$ ) distributed. SADIE also produces an index of clustering ( $V$ ), which measures the degree to which the sampling units cluster into areas of above average cover, that is, a patch ( $V_i$ ), or to areas of below average cover, that is, a gap ( $V_j$ ). Patches are defined as areas where the index of clustering is greater than 1.5 and gaps are defined as areas where the index of clustering is less than  $-1.5$  (Maestre 2003; Perry and others 1999). Again, randomisation tests were used to test if the presence of patches and/or gaps were significant by comparing the mean value of the index of clustering with expectations of 1 for patches or, separately,  $-1$  for gaps.

To determine the strength of the spatial association between litter and perennial patches we used a LISA (Anselin 1995; Perry and Dixon 2002). This calculates the relative contribution of each sampling unit towards ( $\chi_k$ ) the overall correlation coefficient ( $\chi$ ) between perennial plant and litter patch distributions (Perry and Dixon 2002; Maestre 2003). From the SADIE index of clustering ( $V_k$ ), the local spatial association for each unit  $k$  and the overall correlation are determined by (Winder and others 2001; Perry and Dixon 2002)

$$\chi_k = n(V_{k1} - q_1)(V_{k2} - q_2) / \left[ \sum_k (V_{k1} - q_1)^2 \sum_k (V_{k2} - q_2)^2 \right]^{0.5}$$

$$\chi = \left( \sum_k \chi_k \right) / n.$$

Here  $V_{k1}$  and  $q_1$  represent the cluster indices and their mean for the litter patches, while  $V_{k2}$  and  $q_2$

represent the perennial patches. In our study, the total number of sampling units ( $n$ ) was 500 with each unit representing 10 cm of summed binary data from the 5000 point binary data collected on litter and perennial patches at each transect. Positive values of  $\chi_k$  indicate the coincidence of patches or gaps in both litter and perennial patches and gaps, while negative values indicate a misalignment, with a patch occurring in one data set and a gap in the other (Winder and others 2001).

#### *Identifying Potential Drivers of Litter Patch Arrangement*

To test for spatial dependence in the cover of perennial and litter patches, we constructed semi-variograms for both patch types using the 5000 point binary data for each transect. Semi-variograms provide two measures of the spatial characteristic of the data: (1) the nugget ( $C_0$ ), which represents the random variance occurring at a scale less than that used for field sampling, in our case  $C_0$  represents the spatial variation less than 1 cm; and (2) the range ( $A_0$ ), the distance separating sampling points at which semi-variance reaches an asymptote or the maximum range of autocorrelation (Schlesinger and others 1996). In our case, this is the distance over which, for example, the presence of litter at one point is dependent upon the presence of litter at another point. The  $A_0$  is generally correlated with the size of anomalies in the landscape (Schlesinger and others 1996). We expected the  $A_0$  to represent a distance associated with perennial patch or perennial inter-patch size, where perennial patches are the ‘‘anomalies’’ in the landscape. Our semi-variograms fitted well to spherical models, which have been proven useful in the interpretation of two-dimensional spatial data (for example, Wang and others 2007). The spherical models had high  $r^2$ , minimal extrapolation of semi-variance at spatial scale less than 5 cm, and fitted model shape (for example, Wang and others 2007). Semi-variograms were modelled with the GS<sup>+</sup> software Vers. 9 (Robertson 2000).

To compare the spatial indices, we used Permutational Multivariate ANOVA (PERMANOVA). Resemblance matrices were constructed with Euclidean distances and data analysed with 9999 permutations with Type III error rates (Anderson and others 2008). All spatial indices ( $I_a$ ,  $V_i$ ,  $V_j$ ,  $A_0$ ,  $C_0$ ,  $C_0 + C$ ,  $C/(C_0 + C)$ ) with the exception of  $\chi$  were compared in a mixed-models PERMANOVA with community and patch type as fixed factors. The first stratum considered Community and the second stratum Patch and its interaction with Community. Additionally, this allowed us to examine whether

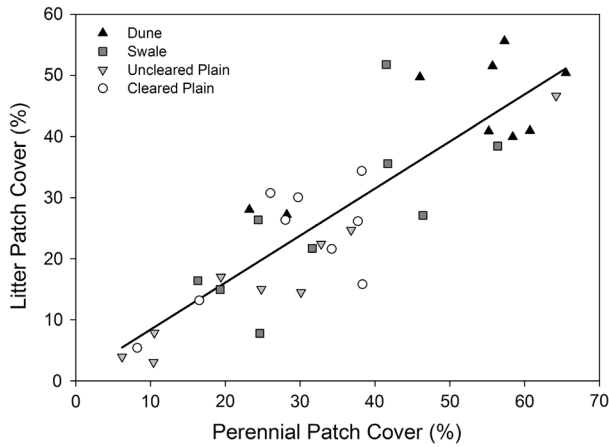
our cleared landscape differed in its spatial properties to its uncleared analogue. We were most interested in the interaction, in order to determine whether the spatial indices for each patch type varied among communities. The degree of association between litter and perennial patches  $\chi$ , in relation to the single fixed factor community, was analysed with a one-way PERMANOVA (Anderson and others 2008).

To determine whether the strength of the association between perennial patches and litter patches differed between perennial patch sizes ( $\chi_{\text{all}}$ ) and types ( $\chi_{\text{tree}}$ ,  $\chi_{\text{shrub}}$ ,  $\chi_{\text{CWD}}$ ), we plotted LISA values ( $\chi$ ) against perennial patch size and fitted a linear regression model for each patch type. Perennial patch size was  $\text{Ln}(x)$  transformed prior to analysis. To further explain the spatial patterns in our data, we considered the semi-variogram range,  $A_0$ . To determine if perennial patches are driving the scale of maximum litter variability, we used a Pearson's correlation to determine the strength of the linear relationship between litter variance (that is, litter range,  $A_0$ ) and the mean and median size of the perennial patches, and the mean and median size of the inter-patch (bare) areas.

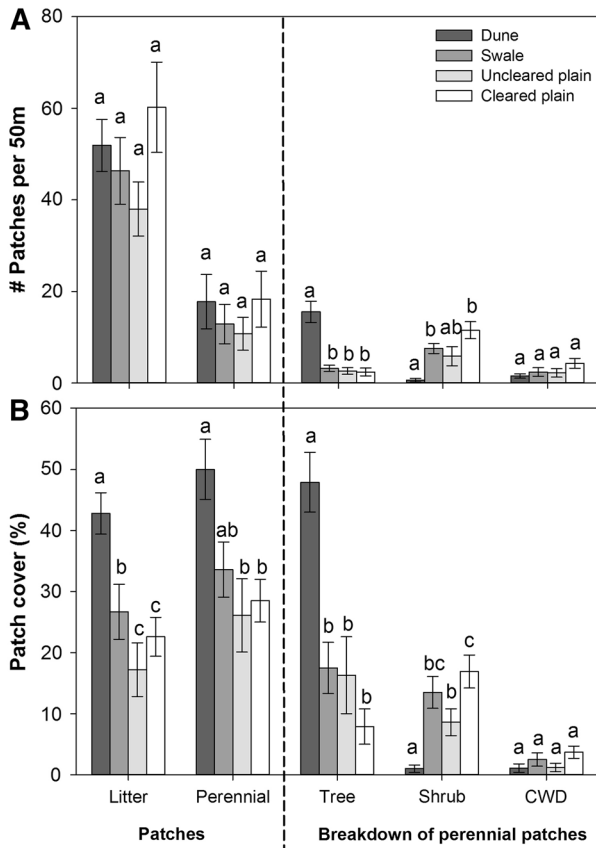
## RESULTS

### Cover of Perennial and Litter Patches

The cover of litter patches clearly increased with increases in the cover of perennial patches ( $F_{1, 34} = 105.00$ ,  $P < 0.001$ ,  $R^2 = 0.76$ ; Figure 1). The number of litter and perennial patches per transect (that is, patch density) did not significantly differ among communities (Litter:  $P = 0.21$ ; Perennial:  $P = 0.09$ ; Figure 2A), however, the contribution of different perennial patch types did. There were significantly more trees in the dune than the remaining communities ( $F_{3, 32} = 23.02$ ,  $P < 0.001$ ; Figure 2A), and significantly more shrubs in the swale and cleared plain ( $F_{3, 32} = 8.81$ ,  $P < 0.001$ ; Figure 2A). The number of coarse woody debris patches did not differ among communities ( $P = 0.16$ ). Perennial patch cover varied significantly among the four communities ( $F_{3, 32} = 3.88$ ,  $P = 0.018$ ; Figure 2B), with the greatest cover in the dunes and the least cover in the uncleared plains. Similarly, the cover of litter patches was also greatest in the dunes, and least in the uncleared plains ( $F_{3, 32} = 5.64$ ,  $P = 0.003$ ; Figure 2B). The composition of perennial patches also varied significantly among communities, with the greatest tree cover in the dunes ( $F_{3, 32} = 13.7$ ,  $P < 0.001$ ) and greatest shrub cover in the uncleared plains



**Figure 1.** The cover of litter patches (% cover) in relation to the cover of perennial patches (% cover). Regression equation: Litter cover (%) = 0.77 × Perennial patch cover (%) + 0.68;  $R^2 = 0.76$ ;  $P < 0.001$ .



**Figure 2.** The **A** count and **B** average cover (%) of litter and perennial patches, and the contribution of each perennial patch type in each community. Within a patch type, different superscripts (LSD) indicate a significant difference in means at  $P < 0.05$ . *Perennial patches* all perennial patches combined, *CWD* coarse woody debris.

( $F_{3, 32} = 28.7$ ,  $P < 0.001$ ; Figure 2b). The cover of coarse woody debris (CWD) did not differ significantly among communities ( $P = 0.11$ ).

### Size Distribution of Perennial and Litter Patches

We found that the truncated power law was the best fit for both litter and perennial patch size distributions when data were summed over each community (Table 1). The degree of truncation, that is,  $1/\beta$ , was much greater in the cleared plain community than its uncleared analogue for both perennial (192.7 cf. 467.6; Table 1) and litter patches (17.8 cf. 30.8; Table 1). Within each community, litter patches were smaller than perennial patches ( $D \geq 0.55$ ,  $P < 0.0001$ ; Figure 3; Appendix 1). The size distribution of litter patches also significantly differed among communities ( $D \geq 0.09$ ;  $P \leq 0.03$ ; Appendix 1 and 2) except between the plain and the cleared plain ( $P = 0.06$ ; Appendix 1 and 2). However, perennial patch sizes were similar among all communities ( $P > 0.06$ ; Appendix 1 and 2), with the exception of swale and cleared plains ( $D = 0.17$ ;  $P = 0.002$ ; Appendix 1 and 2), where perennial patch sizes in the cleared plain were much smaller.

### Spatial Association Between Perennial and Litter Patches

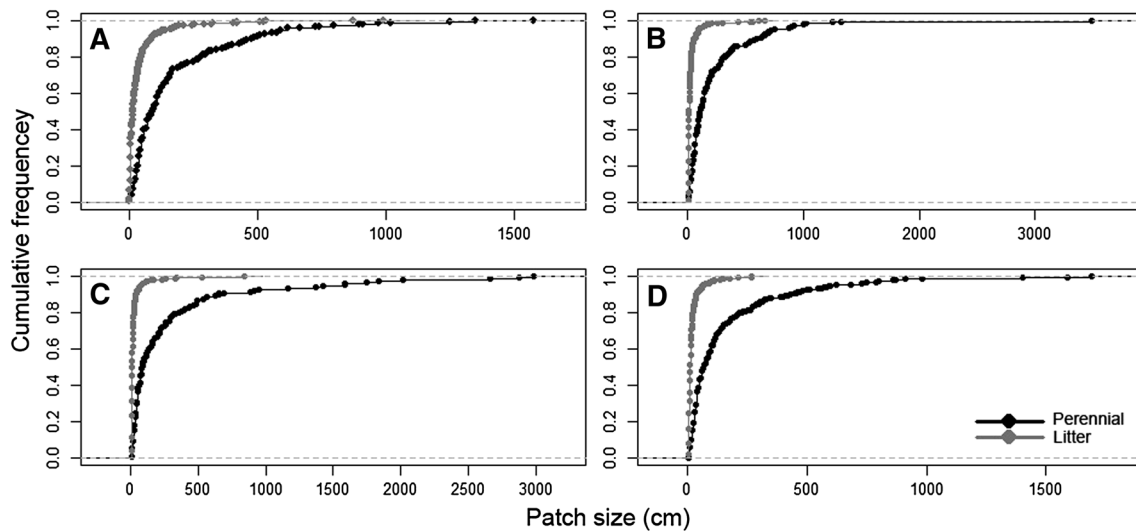
Perennial patches and litter patches were spatially clumped ( $I_a \gg 1$ ; Table 2), with clearly defined “patch” and “gap” configurations for both patch types across all communities ( $V_i \gg 1.5$ ;  $V_j \ll -1.5$ ; Table 2). The index of aggregation and degree of clustering were greatest in the swales and least in the cleared plains for both patch types, although there were only significant differences among communities in the degree of clustering into “patches” ( $V_i$ : Pseudo- $F_{3, 32} = 3.07$ ;  $P = 0.040$ ; Appendix 3). There were no significant differences between litter and perennial patches for any of the other SADIE indices ( $I_a$ :  $P = 0.26$ ;  $V_i$ :  $P = 0.50$ ;  $V_j$ :  $P = 0.56$ ; Appendix 3).

The degree of association ( $\chi$ ) between the perennial patches and litter patches was moderate, with mostly positive correlations between the arrangement of both patch types in all communities (Figure 4; Table 2). There were no significant differences in the degree of association between perennial patches and litter among the communities ( $P = 0.58$ ; Appendix 3). Local association ( $\chi_k$ ) between perennial and litter patches ranged from

**Table 1.** Summary of Size Distribution Model Parameters and Akaike’s Information Criterion

|              | Dune           |                | Swale          |                | Plain          |                | Cleared Plain  |                |
|--------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
|              | Litter         | Perennial      | Litter         | Perennial      | Litter         | Perennial      | Litter         | Perennial      |
| $\gamma$     | 1.35           | 1.219          | 1.395          | 1.211          | 1.433          | 1.216          | 1.418          | 1.231          |
| $\alpha$     | 0.697          | 0.908          | 0.722          | 0.86           | 0.737          | 0.605          | 1.057          | 0.817          |
| $\beta^{-1}$ | 0.017          | 0.005          | 0.025          | 0.004          | 0.033          | 0.002          | 0.056          | 0.005          |
| AIC Pow.     | 4575.64        | 3511.39        | 3717.23        | 2928.88        | 2836.64        | 2278.11        | 4621.89        | 3891.55        |
| AIC TPL      | <b>4361.33</b> | <b>3076.15</b> | <b>3605.09</b> | <b>2576.10</b> | <b>2797.55</b> | <b>2082.47</b> | <b>4264.33</b> | <b>3459.10</b> |

Model parameters for size distributions. Parameters are given for the power law ( $x^\gamma$ ) and a truncated power law with an exponential cut-off ( $x^\gamma \exp^{-\beta x}$ ). Akaike’s information criterion (AIC) values are given for each model. The lowest AIC values are bolded.



**Figure 3.** Cumulative distribution of litter and perennial patch sizes for **A** dune, **B** swale, **C** uncleared plain and **D** cleared plain. Note the X axis varies for each community.

**Table 2.** Summary of SADIE and LISA Indices

| Landform        | Patch type | Index of aggregation |     | Clustering into patches |     | Clustering into gaps |     | Association |      |
|-----------------|------------|----------------------|-----|-------------------------|-----|----------------------|-----|-------------|------|
|                 |            | $I_a$                | SE  | $V_i$                   | SE  | $V_j$                | SE  | $X$         | SE   |
| Dune            | Litter     | 6.48                 | 1.0 | 6.80 <sup>a</sup>       | 1.1 | -7.15                | 1.3 | 0.51        | 0.12 |
|                 | Perennial  | 5.79                 | 0.9 | 5.96 <sup>a</sup>       | 0.9 | -6.66                | 1.3 |             |      |
| Swale           | Litter     | 7.75                 | 1.6 | 9.49 <sup>b</sup>       | 2.2 | -8.60                | 1.8 | 0.64        | 0.06 |
|                 | Perennial  | 7.36                 | 1.4 | 9.44 <sup>b</sup>       | 2.3 | -8.19                | 1.6 |             |      |
| Uncleared plain | Litter     | 6.49                 | 1.1 | 7.17 <sup>a</sup>       | 1.1 | -6.94                | 1.2 | 0.50        | 0.12 |
|                 | Perennial  | 6.14                 | 1.1 | 6.93 <sup>a</sup>       | 1.3 | -6.86                | 1.4 |             |      |
| Cleared plain   | Litter     | 4.58                 | 0.8 | 4.74 <sup>c</sup>       | 1.0 | -4.55                | 0.7 | 0.47        | 0.09 |
|                 | Perennial  | 4.46                 | 0.3 | 4.80 <sup>c</sup>       | 0.5 | -4.61                | 0.4 |             |      |

Summary of SADIE and LISA indices for each patch type and each community. Superscripts indicate significant differences. Peren. = perennial patch,  $I_a$  = index of aggregation;  $V_i$  = index of clustering into patches;  $V_j$  = index of clustering into gaps;  $\chi_i$  = Local Indicator of Spatial Association (LISA).

-12.2 to 28.3 across all communities, with 30% of local associations having a negative value (Appendix 4).

The size of perennial patches did not appear to enhance the strength of their association with litter patches. We found a significant, but weak

( $R^2 \leq 0.06$ ) relationship between perennial patch size and the strength of the local associations for shrub and tree patches (Shrub:  $\chi_{\text{shrub}} = 0.17 \times \text{Ln}(\text{patch size}) - 0.26$ ;  $F_{2, 229} = 3.99$ ;  $P = 0.046$ ;  $R^2 = 0.01$ ; Tree:  $\chi_{\text{tree}} = 0.27 \times \text{Ln}(\text{patch size}) - 0.68$ ;  $F_{2, 229} = 15.79$ ;  $P < 0.001$ ;  $R^2 = 0.06$ ; Appendix 4). We found no evidence for a relationship between CWD size and an increase in local associations ( $\chi_{\text{CWD}}$ ; Appendix 4).

Most perennial patches appeared to accumulate litter (Figure 4), though litter patches did not always occur directly under a perennial patch. Furthermore, larger perennial patches were sometimes associated with a number of smaller litter patches rather than a single large litter patch (Figure 4). This phenomenon was particularly evident in the cleared plains (Figure 4).

### Identifying Potential Drivers of Litter Patch Arrangement

The spatial distribution of litter and perennial patches had a high proportion of structured spatial variance in all communities (structural component:  $C/(C_0 + C) > 0.6$ ; Nugget:  $C_0 < 0.09$ ; Table 3; Appendix 5). However, there were no significant differences in the proportions of spatially structured variance among communities ( $C/(C_0 + C)$ :  $P = 0.16$ ;  $C_0$ :  $P = 0.12$ ; Table 3; Appendix 5). The distance over which patch distributions were autocorrelated (Range:  $A_0$ ), did not differ significantly among communities for either perennial or litter patches (Community:  $P = 0.08$ ; Patch:  $P = 0.09$ ; Table 3; Appendix 5). The cleared plains, however, had the smallest range for perennial and litter patches, indicating that

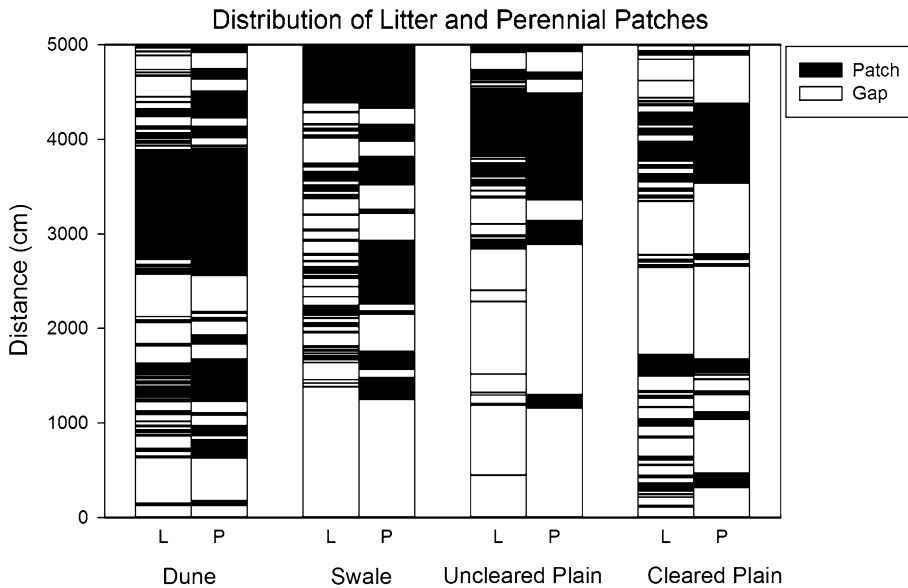


Figure 4. The distribution of litter (*L*) and perennial patches (*P*) at a typical site for each community. The *black* represents the presence of a litter or perennial patch and the *white* indicates the bare inter-patch “gap” area.

Table 3. Summary of Semi-variogram Parameters

| Community       | Patch type | Nugget ( $C_0$ ) | Sill ( $C_0 + C$ ) | Range (m) ( $A_0$ ) | Structural component $C/(C_0 + C)$ | $R^2$ |
|-----------------|------------|------------------|--------------------|---------------------|------------------------------------|-------|
| Dune            | Litter     | 0.069            | 0.28               | 16.66               | 0.78                               | 0.67  |
|                 | Perennial  | 0.041            | 0.24               | 6.02                | 0.84                               | 0.59  |
| Swale           | Litter     | 0.024            | 0.21               | 12.67               | 0.90                               | 0.60  |
|                 | Perennial  | 0.037            | 0.23               | 8.65                | 0.84                               | 0.64  |
| Uncleared plain | Litter     | 0.047            | 0.13               | 11.14               | 0.76                               | 0.60  |
|                 | Perennial  | 0.017            | 0.18               | 8.61                | 0.91                               | 0.68  |
| Cleared plain   | Litter     | 0.010            | 0.16               | 1.60                | 0.95                               | 0.39  |
|                 | Perennial  | 0.086            | 0.20               | 3.86                | 0.60                               | 0.47  |

Averaged semi-variogram parameters for litter and perennial patch data for each community. No significant differences were found between the communities. All models are spherical.



they had the highest spatial variability of the four communities sampled.

With the exception of the cleared plains, the average range of litter was greater than the average range of perennial patches within each community, indicating that perennial patches are more spatially variable than litter patches. Although the semi-variogram range ( $A_0$ ) is often correlated with the average size of physical anomalies within the landscape, we found relatively weak correlations between the range and the mean or median patch size for all four communities ( $r < 0.65$ ; Table 4). Instead, we found significant correlations between the range and the size of the gaps (that is, the unvegetated areas between perennial patches; Appendix 6) for both the swales and cleared plains ( $r > 0.81$ ;  $P \leq 0.01$  Table 4). There were significantly larger distances between perennial patches in the swale and uncleared plain than the dune and cleared plain communities ( $F_{3,349} = 4.12$ ;  $P = 0.007$ ; Appendix 6).

## DISCUSSION

Despite the generally widespread notion that litter tends to accumulate under perennial vegetation (for example, Facelli and Pickett 1991; McElhinny and others 2010), there is limited empirical evidence that self-organising mechanisms also apply to surface litter. Many semi-arid ecosystems show strong evidence of self-organising patchiness resulting from the accumulation of resources under either living or dead perennial plants (Tongway and Ludwig 1990; Eldridge and Wong 2005). In this study, we found that zones surrounding patches of perennial vegetation were weakly associated with patches of surface litter. Both perennial and litter patches exhibited a strong “patch” and “gap” spatial arrangement, and the cover of litter increased linearly with increasing perennial patch cover. We found that there were fewer, but larger, perennial patches than litter patches. When we measured the spatial arrangement of patches at the smallest spatial scale (centimetres), there was only

a moderate spatial association between perennial patches and litter patches. Contrary to our expectation, we did not detect any trend between perennial patch length and the strength of its association with litter, indicating that larger perennial patches did not have stronger spatial associations with accumulated litter than smaller perennial patches. Rather, litter patch size and perennial patch size were best explained by truncated power law relationships, suggesting to us that self-organisation mechanisms play an important role in the spatial structure of the litter, but not necessarily through intense local, positive interactions. Furthermore, we did not find differences between litter spatial patterns among communities, suggesting that self-organisation mechanisms do not vary strongly with local land use or edaphic variations.

## Perennial Patch Cover Reflects Litter Cover

The presence of surface litter is often used as an indicator of enhanced nutrient pools due to its apparent connection with patches of perennial vegetation from which it is derived (Dean and others 1999). Previous studies have shown strong links between perennial vegetation canopy size and associated litter bed dimensions for open woodlands (McElhinny and others 2010; Travers and Eldridge 2012). Building upon this, we found that the density and size, and therefore total cover of perennial vegetation, determines the cover of surface litter, supporting our first hypothesis. Across the range of communities we studied, which varied markedly in their perennial cover and composition, we found a strong positive linear relationship between the percentage cover of perennial patches and the cover of surface litter at a scale of tens of metres.

## Power Laws and the Size Distribution of Perennial and Litter Patches

Power law size distributions occur in a wide range of natural and human-constructed systems (Kefi

**Table 4.** Correlations with Litter Autocorrelation Range

| Correlation with $A_0$  | Dune | Swale | Uncleared plain | Cleared plain |
|-------------------------|------|-------|-----------------|---------------|
| Mean patch size         | ns   | ns    | ns              | ns            |
| Median patch size       | ns   | ns    | ns              | ns            |
| Mean inter-patch size   | ns   | 0.75  | ns              | -0.83         |
| Median inter-patch size | ns   | 0.81  | ns              | ns            |

Pearson’s correlation ( $r$ ) between the litter patch range ( $A_0$ ) and the mean and median patch and inter-patch sizes. For given vales  $P \leq 0.01$ , non-significant results (ns) are also indicated.

and others 2011). We found that the organisation of both perennial and litter patches was consistent with truncated power law relationships. A number of mechanisms have been proposed to explain why patch sizes in ecological systems often follow power laws (for example, Mitzenmacher 2003; Pascual and others 2002). Few of these, however, include mechanisms involving local interactions, which are important for determining the size distribution of perennial vegetation patches in arid systems (Kefi and others 2011). Of these few mechanisms, disturbance–recovery mechanisms likely explain the power law relationships in patch organisation. This mechanism allows disturbance and recovery processes to operate across a range of time scales (Rietkerk and Van de Koppel 2008; Kefi and others 2011). For litter patch formation and distribution, disturbance and recovery mechanisms likely involve physical transport mechanism such as wind and water, which abscise and re-distribute litter (Li and others 2009). Intrinsic differences among communities may further affect mechanisms that drive litter patch formation, as we found that litter patch size distribution was different in the dune compared with the other communities. This may be due to different amounts of surface litter or different leaf shapes among the vegetation communities. Despite these differences in litter patch size distribution, there were no substantial differences among communities in perennial patch size distribution. We also found that litter patch size, while following a truncated power law distribution, was consistently much smaller than perennial patches. Overall, the truncation parameter ( $\beta^{-1}$ ) was an order of magnitude greater in the litter patches than the perennial patches.

The disassociation between larger perennial patch size and associated litter patch size may be due to limited availability of litter, ineffective harvesting of litter from bare, non-patch areas or small-scale, abiotically driven disturbances. For example, perennial plants in water-limited environments are effective at harvesting rainfall and channelling it to their roots. However, if water ponds on the surface at the immediate base of the trunk, litter can be re-distributed away from perennial plants, creating gaps in the litter patch (Mayor and others 2009; McElhinny and others 2010). Small-scale abiotic processes, less than 1 m across, are often overlooked in ecological studies despite their potentially important role in disturbance or recovery processes. Without further modelling, we cannot determine the specific disturbance–recovery mechanisms driving our observations of truncated power law size clusters of litter patches.

## Litter Does Not Accumulate in Perennial Patches by Positive Feedback Mechanisms

Numerous studies have demonstrated that perennial vegetation modifies its environment by accumulating resources at a scale consistent with, or greater than, the area and time that it occupies the landscape (Badano and others 2006). This can affect larger-scale resource distribution (Shachak and others 2008) and spatial patterns within the landscape (Ludwig and others 1999). Accumulation of litter beneath plant canopies is expected to result from small-scale (metres) positive feedback mechanisms (Levin and Segel 1985; Rietkerk and Van de Koppel 2008) or localised processes of disturbance and recovery (Pascual and Guichard 2005) whereby perennial plants create conditions favourable for the accumulation of litter. They could do this by, for example, increasing threshold velocities for the entrainment of organic matter causing litter to be deposited around the bases of perennial plants (Dean and others 1999; Okin and others 2009). However, when we measured patches in fine detail, at a scale of centimetres, perennial patches and their “associated” litter patches were only weakly to moderately spatially associated. Further, we found no apparent increase in the strength of their association with increasing perennial patch size. These observations do not provide support for our third hypothesis that perennial patches facilitate litter accumulation in a positive feedback mechanism at small scales, that is, perennial patches increase litter accumulation, which in turn increases perennial patch size and so on. Despite this, water and other resources may still accumulate through positive feedback mechanisms (Rietkerk and Van de Koppel 2008).

## Perennial Patch Arrangement May Influence the Spatial Variability of Litter Patches

Previous studies have found that the number and spatial arrangement of perennial patches may play important roles in accumulating resources (Tongway and others 2001; Bouma and others 2009). Although perennial patch size alone was not indicative of litter patch size, we did find a significant relationship between litter patch spatial variability and the distance between perennial patches. In the swale, greater distances between perennial patches correlated with a decrease in litter patch variability. However, the opposite trend occurred in the cleared plains, with greater dis-

tances between perennial patches correlating with an increase in surface litter variability. These two communities had similar perennial patch cover, composed of similar types of perennial patches (that is, trees, shrubs, CWD). However, the swale had more surface litter; a larger distance between perennial patches and a much stronger degree of patchiness than the cleared plain. This combination appears to allow a more stable litter landscape to develop. The relatively large distance between perennial patches directly influences the micro-scale fetch length of wind, affecting wind speed and therefore the tendency of wind to entrain litter (Li and others 2009). This likely contributes to the high degree of patchiness, and higher stability in this community. This supports previous findings that inter-patch distance may differ in their importance for resource variability among communities (Ludwig and Tongway 1995).

### A Half-Century Legacy Effect of Land Clearing on Litter

The effects of tree removal and land clearing 50 years prior to measurements resulted in a shift in the composition of perennial patches, with a significant increase in the cover and number of perennial shrub patches. This is consistent with observations of shrub encroachment in many arid and semi-arid ecosystems globally (Eldridge and others 2011). The removal of trees, which persist as decaying logs, created a more spatially variable landscape in terms of perennial patch and litter arrangement than its uncleared analogue. The relationship between litter spatial variability and inter-patch distance remained equal in magnitude but switched to a negative correlation from the unmodified analogue with an equivalent density of shrubs (swale). This could suggest that alternative disturbance and recovery processes are occurring in the modified system. For example, wind dynamics may be altered in an environment with denser shrubs, which may affect aeolian processes associated with litter movement (for example, abscission, transportation and so on). However, given that shrub density has increased at the expense of trees, litter may be more variable in this landscape due to the type of litter and amount of litter produced by these species.

It appears that shifts in vegetation cover will affect the surface cover of litter, irrespective of whether the ecosystem has been subjected to clearing-induced vegetation change. Modifying vegetation structure and composition may have long-term effects on relationships between litter

accumulation and perennial patch size and arrangement. Without a clear understanding of what drives the organisation of surface litter, it is difficult to understand how processes related to nutrient cycling and availability might shift with vegetation modification.

### CONCLUDING REMARKS

Our study illustrates that the spatial association between perennial patches and litter patches is more complex than has been generally reported (for example, Shachak and others 2008). Although there were strong relationships between the percentage cover of perennial and litter patches, we detected only weak to moderate spatial association between them when measured at a fine scale. It is likely that both the litter and perennial patches are subject to self-organisation mechanisms, but the drivers of spatial arrangement are likely different. The nature of the size distribution of litter patches suggests that self-organisation mechanisms are operating. As we found no evidence that litter accumulates with perennial patches in a scale-dependent feedback, it is likely that litter spatial arrangement is driven by disturbance-recovery mechanisms. This does not however, exclude the possibility of other resources associated with perennial patches accumulating via scale-dependent feedbacks. The distance between perennial patches in shrub-dominated communities appears to have strong effects on litter spatial variability. However, this relationship appears to be sensitive to modification of vegetation structure and composition, such as tree clearing. Determining what drives the variability in patch spatial arrangement among communities, and between perennial patches and litter within semi-arid plant communities, has important implications for the application of self-organisation models to real ecosystems.

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