Long-term influence of fallen logs on patch formation and their effects under contrasting grazing regimes

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Abstract   Patchiness is a critical functional feature of arid lands, increasing productivity and diversity, but there is little information on the long-term dynamics of patch formation. While plant-created heterogeneity is widespread, grazing reduces plant density, hence removing patchiness. Patchiness is also associated with fallen logs and it is particularly important to assess this association in grazed areas, as there are few patches which are not created by living plants. We studied differences in soil nutrient content and soil seed bank associated with the presence of logs in the long ungrazed Koonamore Vegetation Reserve and an adjacent heavily grazed paddock in chenopod shrublands of South Australia. We studied soil properties associated with fallen logs of unknown age, and others known to have persisted for up to 78 years. Logs acted as traps for soil nutrients and seeds. Organic carbon was higher in soils associated with logs, and also higher inside the reserve than in the grazed paddock. Propagule number and species richness were higher next to logs than in open spaces and viable seeds were in much higher abundance next to logs in the grazed paddock than any other site. Increased time *in situ* of a log had a relatively small effect on soil organic carbon and total nitrogen. Logs act as resource traps which may enhance the diversity of the system, and may be particularly important for maintaining patches of resources in areas of severe grazing damage. Hence, their preservation should be incorporated into management schemes. [Correction added on 3 March 2015, after online publication: The following parts in the abstract have been edited. 'Organic carbon and total nitrogen were higher in soils associated with logs' has been corrected to 'Organic carbon was higher in soils associated with logs', and 'had a relatively small effect on soil organic carbon, total nitrogen and available potassium' has been corrected to 'had a relatively small effect on soil organic carbon and total nitrogen'.]

Key words: arid land, grazing exclusion, nutrient accumulation, resource heterogeneity, seed bank.

INTRODUCTION

Patchiness of resources has been extensively studied in arid lands because its presence strongly affects productivity and diversity of arid systems (Noy-Meir 1985). Studies investigating resource patches include patches associated with trees (Facelli & Brock 2000), shrubs (Schlesinger *et al.* 1996; Facelli & Temby 2002), succulents (Stock *et al.* 1999), grasses (Tongway & Ludwig 1994), animal diggings (Shachak *et al.* 1991; James *et al.* 2009) and fallen logs (Tongway *et al.* 1989; Bowman & Facelli 2013). However, there is very little information about how patches change over time (but see Barnes & Archer 1996; Facelli & Brock 2000). Since these systems can be modelled as dynamic patchworks with patches being formed and then dissipating, information about patch dynamics is critical to enhance our understanding and ability to manage them.

Patch dynamics is controlled by movement of materials from open spaces and accumulation in small depressions or around structures (e.g. shrubs, trees, logs) that capture and retain the transported materials (Ludwig & Tongway 1995). Grazing alters community structure and ecosystem function by reducing vegetation cover through defoliation and subsequent reduced biomass production (Popp *et al.* 2009). Low densities of plants can cause increased surface water flow leading to erosion, decreasing infiltration rates and lowering of the number of resource patches (Sparrow *et al.* 2003). Hoof action by grazers causes soil crust destruction, altering the hydrological functioning of arid land systems, and disrupting or even eliminating the function of resource patches (Eldridge *et al.* 2000; Heshmatti *et al.* 2002).

Changes in resource patchiness under heavy grazing can also reduce seed availability and hence limit the recruitment of many species in arid ecosystems (Kinloch & Friedel 2005a; Solomon *et al.* 2006; Kassahun *et al.* 2009). Water and wind movement often accumulates seeds in resource patches along with nutrients and water (Aguiar & Sala 1999). In fact, seed density can increase ten-fold and seedling emergence threefold under shrubs, compared with open

spaces (Osem *et al.* 2007). Low seed availability can be caused by reduced seed output by adult plants due to grazing (Hunt 2001). While many studies find a reduction in seed bank due to grazing degradation, there is conflicting evidence regarding soil seed banks in arid lands under grazing: one study by Osem *et al.* (2007) found an increase in soil seed reserves with heavy grazing degradation, while other studies have found no such changes (Meissner & Facelli 1999; Osem *et al.* 2006).

Resource patches provide favourable sites for seedling establishment, and the loss of patches affects the recovery of vegetation through impacts on soil seed reserves (Kinloch & Friedel 2005b). Seedling establishment and survival is poor in open spaces in arid lands, while resource heterogeneity provides safe sites for seedling establishment (Maestre *et al.* 2003). Changes in soil and vegetation as a consequence of grazing can lead to a lack of vegetation recovery even after resting periods of several years (Friedel *et al.* 2003; Sinclair 2005; Lesschen *et al.* 2008).

Restoration of degraded arid lands is difficult and it is suggested that to restore degraded arid lands resource patches should be reconstructed (Sparrow *et al.* 2003). However, while many studies have looked at the presence of patchiness, little is known about the processes which form these patches. Ludwig and Tongway (1995) suggested that resource patchiness is created by both water and wind erosion of soils and subsequent deposition next to features (such as shrubs and logs) in the landscape. A subsequent study (Tongway & Ludwig 1996) supported this, as branches placed on the ground accumulated soil and increased soil nutrient contents over a 3-year period. Studies by Emmerson *et al.* (2010, 2012) have shown that seeds are also subject to this movement and subsequent deposition in the landscape. However, few studies have looked at patch formation over long time frames. Using space-for-time substitution, Facelli and Brock (2000) studied the resource patchiness created by the *Acacia papyrocarpa* tree and how this patchiness changes with the age of a tree, varying from juvenile to death (at an estimated 400 years). They found the development of the patch is slow (up to 100 years), which suggests that this process of patch development is very different to that caused by non-living features, as reported by Tongway and Ludwig (1996).

Most documented resource patches are associated with living plants but the abundance of these is reduced under heavy grazing. Fallen logs are one of few documented non-living structures in arid lands which contribute to resource heterogeneity, making them unique in their role as patch-creating structures. Logs are known to increase soil nutrient contents and increase seedling emergence and biomass (Bowman & Facelli 2013), yet we do not know how the patchiness of fallen logs changes with time *in situ*.

The objectives of our study were to use a long-term study site (Koonamore Vegetation Reserve) to assess the patterns of development of patches around logs known to have fallen at different times (between 12 and 78 years before the study). We also wanted to determine to what extent fallen logs act as resource accumulators in both near pristine and heavily grazed areas. We specifically chose to focus on soil nutrients and seed banks. We conducted the research in the Koonamore Vegetation Reserve and its adjacent grazed South Lake paddock. The key questions we chose to ask were: (i) 'Is there any difference in heterogeneity associated with fallen logs both inside the reserve and in the grazed paddock?' and (ii) 'How do soil properties and soil seed bank change with time *in situ* of a log on the ground?'

METHODS

Site selection

This study was carried out in the TGB Osborn Vegetation Reserve (hereafter referred to as Koonamore Vegetation Reserve) and the adjacent South Lake paddock of Koonamore Station. The Koonamore Vegetation Reserve is located in the centre of Koonamore Station, 400 km northeast of Adelaide, South Australia (32°15′S, 139°27′E). The 4-km^2 reserve was set up in 1926 to exclude sheep and rabbit grazing (the latter only achieved in the mid-1970s) and follow the changes in vegetation which had been severely overgrazed (Sinclair 2005). The area consists of a complex of low sand dunes alternating with sand plain and harder loam soils with travertine limestone on the intervening flats. The climate of the area is arid, with average yearly rainfall around 200 mm. The vegetation is chenopod shrublands with scattered trees, including *Myoporum platycarpum* R.Br., *Acacia aneura* Benth., *Casuarina pauper* F. Muell. and *Alectryon oleifolius* (Desf.) S.T.Reynolds. Chenopod shrubland communities include *Atriplex vesicaria* Benth., *Atriplex stipitata* Benth. and *Maireana sedifolia* (F. Muell.) Paul G. Wilson. For more details of the reserve, see Osborn (1925) or Sinclair (2005).

The Koonamore Vegetation Reserve (reserve) and adjacent South Lake (grazed) paddock were selected for the study of patch dynamics associated with fallen logs, as not only do both sites have abundant fallen logs, but the contrast in grazing intensity between the sites is stark: the reserve is in near-complete recovery to assumed pre-pastoral condition, while the grazed paddock is heavily degraded. We are aware that our study confounds site with grazing status but the uniqueness of the Koonamore Vegetation Reserve makes it impossible to fully replicate our design. We are confident, however, that differences between the reserve and the grazed area can be mainly attributed to grazing condition. This is based on the existence of a long-term study (started in 1926) indicating that then the vegetation inside the reserve was very similar to today's vegetation in the grazed area, the similarity of environmental conditions (across fence comparison) and the profound differences between grazed and reserve sites.

The north-western side of the reserve and the adjacent area of grazed paddock were selected for transects, as this area has little topographic gradient (less than 5%) and has no sand dunes, and records show that these sites initially possessed similar vegetation structure.

Logs used in the study were 3–5 m in length, 20–40 cm in diameter and of simple branching structure so to be able to match them across sites. At each selected log, a section of adjacent bare ground was also randomly selected approximately 5 m from the log and away from any other living or dead plant.

Patch dynamics

To assess soil nutrient contents next to logs and in open spaces, soil samples were collected for analysis on 5 May 2011. Samples were taken to 5 cm depth and with a 9 cm diameter at each of 10 fallen logs and adjacent open spaces in the reserve, and a further 10 pairs of log and open in the grazed paddock. While slope was usually negligible, if slope was present, samples were collected uphill of the fallen log. Two samples at each site were mixed as a composite sample and sent to Cummings Smith British Petroleum (CSBP) soil and plant laboratory (Western Australia) for determination of soil organic carbon, total nitrogen, nitrate nitrogen, ammonium nitrogen, available phosphorus, available potassium, electrical conductivity, pH and sulphur.

To assess the soil seed bank, at all 20 selected logs and adjacent bare ground sites, one soil sample (as above) was used to assess the extractable seed bank. Seed extraction was conducted as per Malone (1967). All propagules were counted and identified using the seed collection maintained by the Terrestrial Plant Ecology group of The University of Adelaide. A cut test was then conducted on all propagules to determine if they contained a viable seed or not. In addition to the 20 logs, a further 10 logs (five inside the reserve and five outside) were sampled (as above) at both log and open space sites and used to assess the germinable soil seed bank. The two samples were mixed with the volume of one sample (as above) of commercial sand, to reduce soil aggregation. Each processed sample was placed into a tray on 21 May 2011 and watered regularly to promote germination of all non-dormant seeds. Seedling emergence from the soil was recorded and species were identified whenever possible. The experiment was concluded on 11 July 2011.

Time *in situ*

To determine if age or origin of the log affects accumulation of seeds or resources in the patch, we selected fallen logs using the long-term data collected from the Koonamore Vegetation Reserve and later analysed by Sinclair (2004). Records of time since logs had fallen were used to select logs of varying time *in situ* for *M. platycarpum* (29–78 years) and for *A. aneura* (12–75 years).

Four soil samples were collected on 30 August 2011 (as above) at each of 19 logs. When logs were in a site with some slope, samples were collected uphill of the fallen log. Two of the soil samples were mixed into a composite sample and

sent to CSBP soil and plant laboratory (Western Australia) for analysis as per our patch dynamics samples. The two remaining soil samples were mixed as an aggregate and used to assess germinable soil seed bank. Each sample was potted on 5 September 2011, and all pots were watered regularly to promote germination of all non-dormant seeds. Seedling emergence was then quantified and species were identified where possible. The experiment concluded when no new seedling emergence had occurred on 10 October 2011.

Statistical analyses

Soil nutrient and seed bank data were analysed in Graph Pad Prism 6.0. Brown–Forsythe tests were run to determine if standard deviations were significantly different. Data for organic carbon were log transformed for analysis, and total propagules, propagule species richness and viable seed data were square root transformed to equalize variances. We then ran split-plot analyses of variance, and where an interaction was present, a post-hoc Tukey's multiple comparison test was run.

Seedling emergence in the glasshouse was analysed using Graph Pad Prism 6.0 and Pcord5. When the data failed the Brown–Forsythe test for equal standard deviations and transformation did not adequately adjust the data, a two-way nested non-parametric MANOVA was used to determine any differences between treatments.

Time *in situ* data were analysed in Graph Pad Prism 6.0 using linear fits for soil nutrient content against time *in situ*. All data were tested for departure from linearity (runs test) and departure from normality in residuals (D'Agostino-Pearson omnibus test). We chose to use a robust fit for the line of best fit due to departure from normality in our data and did not remove outliers as we consider these points part of the natural variation of this system.

RESULTS

Patch dynamics

The concentration of organic carbon in soils was higher next to logs than in open spaces ($P = 0.007$, Fig. 1a) and higher inside the reserve than in the adjacent grazed site ($P = 0.018$, Fig. 1b), and no significant interaction was found ($P = 0.84$). An interactive effect was detected for total soil nitrogen, showing higher concentrations next to logs in the reserve than in open spaces in the grazed paddock ($P = 0.014$, Fig. 2a); no differences were found between all other combinations of treatments. An interactive effect was also detected for available phosphorus (Fig. 2b), with soil next to logs inside the reserve having higher available phosphorus than open space soils inside the reserve ($P = 0.026$). No significant association was detected for all other soil tests. [Correction added on 3 March 2015, after online publication: 'having higher available phosphorus than all other sites ($P =$
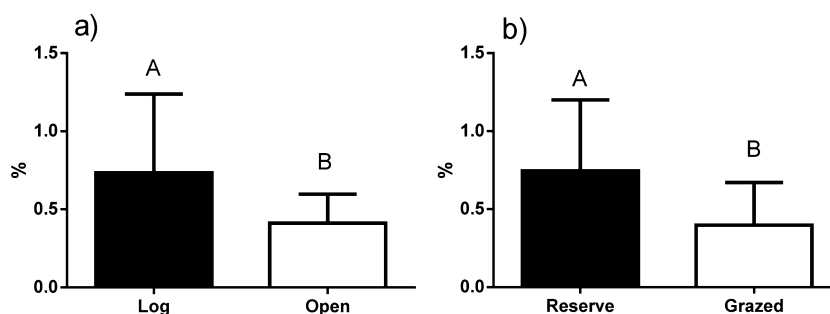
Fig. 1. Organic carbon from soil collected (a) next to logs and in open spaces and (b) in the reserve and grazed paddock (bars indicate SD; capital letters indicate significant difference, $P = 0.007$ and $P = 0.018$, respectively; split-plot two-way ANOVA, data log transformed for analysis).
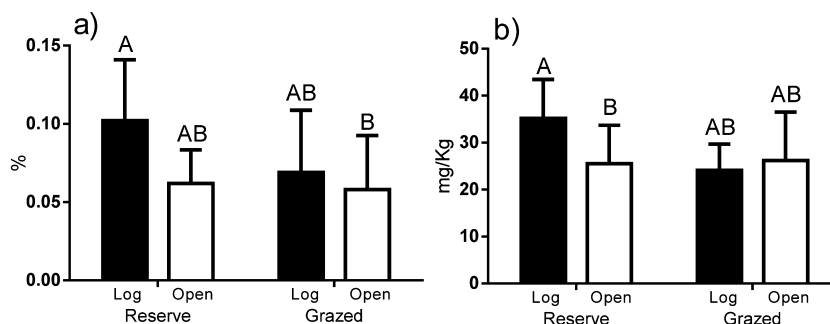

Fig. 2. (a) Total nitrogen and (b) available phosphorus next to logs and in open spaces, in the reserve and grazed paddock (bars indicate SD, capital letters indicate significant difference, $P = 0.014$ and $P = 0.026$; split-plot ANOVA and Tukey's multiple comparison test).

0.026)' has been corrected to 'having higher available phosphorus than open space soils inside the reserve ($P = 0.026$)' in the above statement.]

We found more propagules in soils next to logs than in open spaces, with an interactive effect showing more propagules next to logs in the grazed paddock than in the reserve ($P = 0.009$, Fig. 3a). Species richness of propagules was higher next to logs than in open spaces ($P < 0.001$, Fig. 3b), and no interaction or difference between sites was found ($P = 0.18$ and $P = 0.27$, respectively). Total number of viable seeds was higher in soil next to logs in the grazed paddock compared with all other sites ($P = 0.009$, Fig. 3c); additionally, an interactive effect was found with more viable seed species next to logs in the grazed paddock than all other sites ($P = 0.020$, Fig. 3d).

Numbers of emerged seedlings and seedling species richness in the glasshouse were both greater in soil collected next to logs than from soil collected in the open ($P < 0.001$ and $P < 0.001$, Fig. 4a,b, respectively).

Time *in situ*

Nutrient analyses of soils collected at logs of different ages showed weak evidence for slightly increasing

organic carbon ($P = 0.090$, slope = 0.004, Fig. 5a) and available nitrogen ($P = 0.086$, slope = 0.001, Fig. 5b) with increased time *in situ*. No significant association was detected for available phosphorus or potassium (Fig. 5c,d). Logs of varying time *in situ* were found to have no effect on seedling emergence from soils.

DISCUSSION

Our data suggest that logs are particularly important in creating patchiness in heavily grazed arid lands. Similar to previous work on fallen logs by Bowman and Facelli (2013) and earlier by Tongway *et al.* (1989), we found increases in soil organic carbon and nitrogen as well as higher plant numbers next to logs. The stark contrast found in both soil nutrients and seed bank between log and open space sites provides important information on the properties of patchiness created by logs. We did find surprisingly little difference between logs *in situ* for times ranging from 12 to 78 years (Fig. 5), which suggests that the most intense changes occur during the first decade after the log falls to the ground.

The presence of introduced grazers can cause greater mobilization of soil resources (Tongway *et al.* 2003), and this can result in a net loss of resources from an
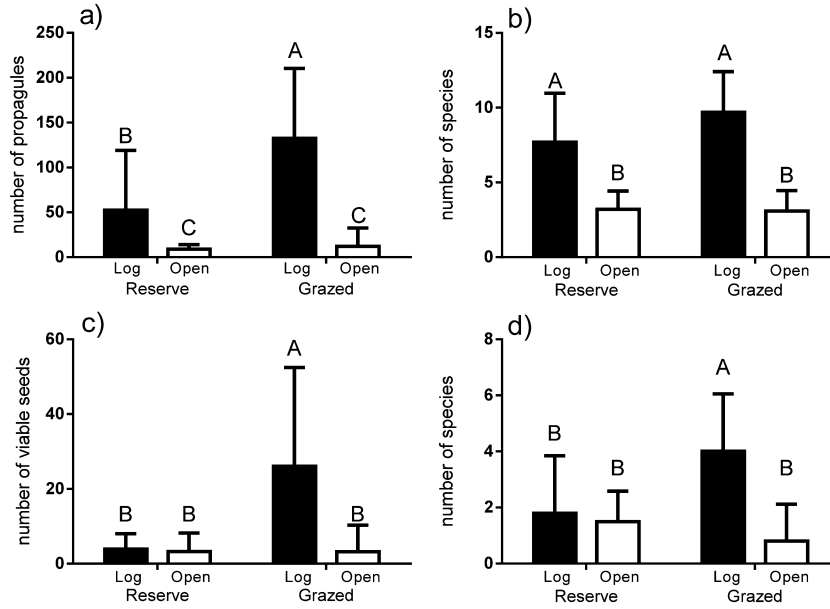
Fig. 3. (a) Total number of propagules, (b) species richness of propagules, (c) total viable seeds and (d) viable seed species richness, all next to logs and in open spaces, in the reserve and grazed paddock (bars indicate SD, capital letters indicate significant difference, $P = 0.009$, $P < 0.001$, $P = 0.009$ and $P = 0.020$; split-plot ANOVA and Tukey's multiple comparison test, (a), (b) and (c) square root transformed for analysis).
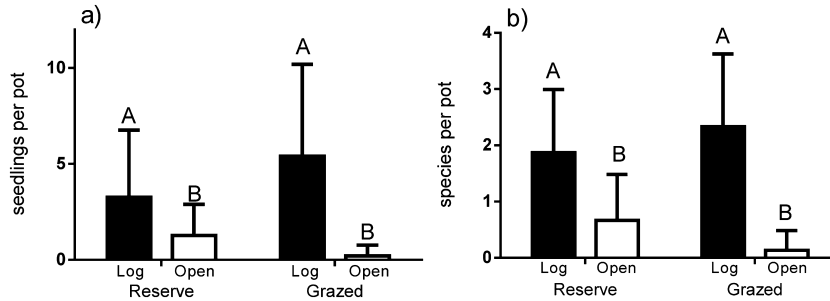

Fig. 4. (a) Number of emerged seedlings and (b) seedling species richness for emerged seedlings in the glasshouse for soils collected next to logs and in the open, and in the reserve and grazed paddock (bars indicate SD, capital letters indicate significant difference, $P < 0.001$ and $P < 0.001$; two-way nested per MANOVA).

entire paddock (Sparrow *et al.* 2003). We suggest that this is occurring in the grazed South Lake paddock, as we found that soil organic carbon was lower in the heavily grazed paddock than in the vegetation reserve, highlighting that fallen logs may be particularly important for creating patchiness in degraded areas, as they could reduce the total export of nutrients by act as sinks. [Correction added on 3 March 2015, after online publication: 'soil organic carbon and total nitrogen were lower' has been corrected to 'soil organic carbon was lower' in the above statement.]

We originally expected the seed bank patterns to mirror soil nutrient concentrations. The higher number of plants inside the reserve should contribute more seeds to the seed bank; hence, we expected more seeds next to logs inside the reserve than in the grazed paddock. A reduction in the soil seed bank could be caused by reduced seed output by adult plants due to grazing (Riginos & Hoffman 2003) and grazing has a negative impact on the number of resource traps which would lower the soil seed bank (Kinloch & Friedel 2005b). However, this was not the case. We suggest that the higher number of seeds in the seed bank next to logs in the grazed paddock is a function of four main processes: (i) a greater mobilization of seeds as a result of trampling by grazers (see Emmerson *et al.* 2010), (ii) a loss of resource patches (by reduction of plant cover), and hence structures which trap seeds, (iii) a favourable microclimate next to logs that increases plant establishment, hence re-contributing seeds back into the patch, and (iv) more weedy plants present under grazing producing larger seed numbers.

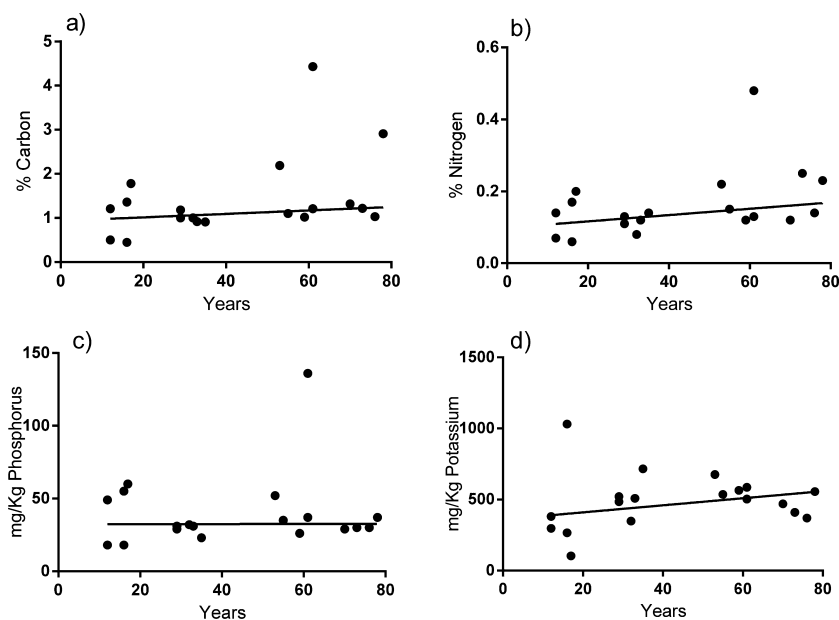Few studies have looked into the mobilization of seeds once they are on the ground. However,

Fig. 5. Linear regressions of (a) organic carbon ($r^2 = 0.16$, slope = 0.0039, $P = 0.0898$), (b) total nitrogen ($r^2 = 0.16$, slope = 0.0009, $P = 0.0855$), (c) available phosphorus ($r^2 = 0.01$, slope = 0.0024, $P = 0.6707$) and (d) available potassium ($r^2 = 0.01794$, slope = 2.484, $P = 0.5846$) associated with fallen logs of varying time *in situ* inside the Koonamore Vegetation Reserve.

Emmerson *et al.* (2010) studied the movement of *Erodiophyllum elderii* seed heads both inside the Koonamore Vegetation Reserve and in the adjacent grazed paddock. They found dispersal to be greatly limited inside the reserve with maximum distances recorded to be just over a metre, while seed heads were more likely to move farther outside the reserve in paddocks subject to sheep grazing, especially along animal tracks (Emmerson *et al.* 2012). A greater mobilization of seeds in the grazed paddock could result in seeds moving further before being trapped in a patch, or even potentially being lost from the paddock.

We found no effect of time *in situ* of fallen logs for emerged soil seed bank, but this is not unexpected, as only a small fraction of arid annual plant seeds survive between years (Pake & Venable 1996). Despite large variation within patches, we still found some evidence of time *in situ* of fallen logs changing soil total nitrogen and organic carbon. We suggest that important soil changes occur in the first decade after a tree falls. However, the 'youngest' fallen log represented in our analysis was 12 years *in situ*. We propose that soil nutrients increase during the first decade *in situ* and then remain fairly constant for the life of the log. [Correction added on 3 March 2015, after online publication: 'in situ of fallen logs changing soil total nitrogen, organic carbon and available potassium' has been corrected to 'in situ of fallen logs changing soil total nitrogen and organic carbon' in the above statement.]

Fallen logs are one of few sources of patchiness which withstand grazing impacts and are thus important in preventing soil nutrients and seeds from leaking

from the system. Recovery in arid lands depends on reconstructing the landscape's natural heterogeneity (Sparrow *et al.* 2003) and as log patches appear to form quickly, the introduction of logs to grazed areas may be an important solution for overcoming the loss of patches. Fallen logs are particularly important for maintaining patches of resources in areas of grazing damage as a refuge for nutrients and particularly seeds; hence, their preservation should be incorporated into management schemes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Output tables for statistical analyses.