The dynamics of formation and dissipation of patches associated with fallen logs in a chenopod shrubland of southern Australia

Alexandra S. Bowman and José M. Facelli



Final report for Australian Flora Foundation

December 2015

Abstract

Resource heterogeneity is a prominent feature of arid ecosystems, yet little is known about the dynamics of patch formation or their dissipation. We aimed to assess patch formation and dissipation associated with introducing and removing fallen logs. We introduced logs and artificial logs to open spaces and assessed changes to soil nutrient contents and annual plant communities after three years. Pairs of fallen logs were also selected and one of each pair was removed. We deployed soil temperature and moisture probes and collected soil samples to determine dissipation of soil nutrient contents and soil seed bank over one year. Three years was not long enough to change soil nutrient contents or annual plant communities when introducing logs, but unplanned destocking had strong effects on soil nutrient contents. The removal of logs produced immediate changes to the soil microclimate, but accumulated nutrients and seeds in the soil remained after one year. Patch formation next to logs occurs between 3 and 12 years *in situ*. Additionally, the removal of logs creates patches that are unique to any others, but the role of this new patch type in the system is unknown, as is the length of its persistence.

Introduction

The presence and functional importance of resource heterogeneity in arid lands is well established. If resources were distributed homogenously throughout arid systems, little or no productivity would occur, however, the presence of resource patches increases the productivity of the whole system (Noy-Meir 1985). These patches can be associated with trees (Facelli & Brock 2000), shrubs (Facelli & Temby 2002), grasses (Tongway & Ludwig 1994), animal diggings (James *et al.* 2009) and fallen logs (Tongway *et al.* 1989; Bowman & Facelli 2013). Generally these studies of patches have largely focused on documenting the existence and characteristics of patches, but there is relatively little information available on how these patches form or dissipate over time. Patchiness is an important driver of plant

productivity and diversity of arid systems (Noy-Meir 1985), hence information about patch dynamics is critical to enhance our understanding and ability to manage them.

The formation of patches has been suggested to be driven both by biotic and abiotic processes. Ludwig and Tongway (1995) suggest that resource patches are created by both water and wind erosion of soils and subsequent deposition next to features in a landscape, such as shrubs and logs. Studies by Emmerson *et al.* (2010; 2012) showed similar transport and subsequent deposition in the landscape also occurring with seeds. Additionally, while

modelling seed dispersal in patchy landscapes, Thompson *et al.* (2014) demonstrated that a large increase in friction factor associated with the presence of vegetation leads to final seed resting positions being largely tied to vegetation distribution. This deposition of materials has been demonstrated in studies which have reported a substantial and rapid accumulation of soil within experimental plots with vegetation and branches (Tongway & Ludwig 1996; Reid *et al.* 1999). However, a patch formed by living plants can be much more complex than one formed by inert structures, as plants can directly modify their environments. Plant root systems can modify soil nutrient and moisture contents through resource acquisition (Sala *et al.* 1989) and hydraulic lift (Horton & Hart 1998). Plant canopies can change light availability and temperature (Facelli & Brock 2000), and dead plant material can change many soil properties (Facelli & Pickett 1991). While some studies have considered how patches may form, information about the timing of patch formation is largely absent from the literature.

Very few studies have looked into dynamics of patch formation. Facelli and Brock (2000) used space-for-time substitution to assess the resource patchiness created by the *Acacia papyrocarpa* tree and how this patchiness changed with the age of a tree. They found the development of the patch is slow (up to 100 years) around this long lived tree (maximum age estimated conservatively at 400 years). In contrast, Tongway and Ludwig (1996) found changes in soil nutrient contents after introducing branch piles for just three years, and Bowman and Facelli (2013) found increased annual plant species diversity on introducing logs to open spaces after just four months.

Similarly, very little information is available on the dissipation of patches. It has been suggested that soil nutrient patches can remain after a patch forming entity is removed (Callaway *et al.* 1991; Barnes & Archer 1996). A few studies have quantified this: Facelli and Brock (2000) found that patch soil nutrient contents remain higher than in adjacent open spaces for at least fifty years after the death of a long lived tree; Tiedemann and Klemmedson (1986) found nutrients to remain at least thirteen years after canopy removal; and Bechtold and Inouye (2007) found soil nutrient contents decreased six years after they removed the canopy of a shrub. Again, all of these studies involved living patch forming entities, and patch dissipation after the removal of a non-living patch forming structure, such as a log, may elicit different results.

Fallen logs are a unique patch forming entity, as they are one of few that are non-living. Fallen logs increase soil nutrient contents, lower volumetric water content and increase annual plant numbers (Bowman & Facelli 2013). Patches formed by logs can be particularly important in grazed areas, as grazing reduces vegetation, thus increasing transport of material, and reduces the number of resource patches, disrupting or even negating the function of resource patches (Heshmatti et al. 2002; Sparrow et al. 2003; Popp et al. 2009). 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). To restore degraded arid lands resource patches need to be reconstructed (Sparrow et al. 2003). Fallen logs are known to create patches (Bowman & Facelli 2013) and their introduction to grazed areas could help to re-establish patches. Additionally, it has been noted that fallen logs are a major resource which are often removed from natural ecosystems for use as firewood (Vázquez et al. 2011). Hence we query the effects of both formation and dissipation of a patch associated with fallen logs. Another study using long term information in a similar system suggested that patches around logs reach a fairly stable condition 12 years after a log falls to the ground (Bowman et al. in press). This suggests that there must be some rapid changes and strong accumulation of materials soon after a log is deposited.

The objectives of our study were to assess the dissipation and formation of patches associated with fallen logs. We chose to focus on short term effects on soil properties. We conducted our research at the Middleback Field Research Centre in South Australia. The key questions we chose to ask were: i) are there any changes in soil microclimate after removal of a fallen log over a one year period, and ii) are there any changes to soil nutrients and annual plant communities associated with the introduction of fallen logs into open spaces over three years. In addition we introduced artificial logs (PVC pipes) of similar diameter to the natural logs to determine if the decomposition of log material contributed to the formation of patches.

Methods

Our study was conducted at Middleback Field Research Centre, 16 km North West of Whyalla, South Australia ($32^{\circ}57$ 'S, $137^{\circ}24$ 'E). The climate of the area is arid, with average yearly rainfall around 230 mm. Rainfall is concentrated in the winter months (June-August), which drives the growth of a diverse annual plant community. The winters are mild (July mean 16.9° C) while the summers are hot (January mean 30.2° C) and usually dry, but can be punctuated by drenching rains during La Niña events. The soils are predominantly brown

calcareous earths with clay-loam texture, and have calcium carbonate accumulated at variable depths. The pH is slightly alkaline, and nutrient availability is generally low (Crocker 1946). The vegetation at the study site is open woodland dominated by *Acacia papyrocarpa* Benth. with chenopod understorey; *Atriplex vesicaria* Heward ex Benth., *Maireana pyramidata* (Benth.) Paul G. Wilson and *Maireana sedifolia* (F. Muell.) Paul G. Wilson dominate the understorey (Facelli & Brock 2000). A large number of annual plant species, both native and introduced can be found, and the guild is presently dominated by *Carrichtera annua* (L. Aschers.), an introduced plant from the Mediterranean (Facelli *et al.* 2005). Throughout the area dead individuals of *A. papyrocarpa* are common and the logs frequently found on the ground most likely belong to this species.

Dissipation of a patch

The Two Mile Paddock was selected for this part of the study, as while there is some grazing degradation the environment is otherwise homogenous and there is an abundance of fallen logs. To determine any changes when removing a log from its environment existing fallen logs (pieces of wood 2.5-4 m long and 10-30 cm diameter, henceforth referred to simply as "logs") were located in the paddock on 24 Mar 2013. We selected logs to be comparable: they had very simple structure, fairly straight, with few or no branches and had no sign of decay. Logs were present at a variety of orientations. Logs were selected in pairs with an adjacent open space area, leaving a minimum 3 m distance from logs and away from any other living or dead plants. The position on the ground of one of each pair of logs was marked out using roofing nails and then the log was removed (henceforth referred to as "removed log"). For the duration of the experiment the site of the removed log was always treated as if the log was still present. The remaining log was left *in situ*. Ten replicates of log, open space and removed log were used for this part of the study.

To assess any changes in microclimate associated with the removal of fallen logs, 5TM© soil temperature and moisture probes (Decagon Devices) attached to EM50© data loggers (Decagon Devices) were deployed at six sets of log, open space and removed log sites. Soil probes were deployed at 5 cm depth in open spaces, immediately adjacent to logs and next to removed logs. The data loggers were set to measure soil temperature (°C) and soil volumetric water content (%) every hour from 23 March 2013 until 22 May 2014.

To assess any dissipation of accumulated nutrients and seeds from the patches around fallen logs, soil samples were collected for further analysis. Soil collection from removed log sites was treated as if the logs were still present, thus soil was collected immediately adjacent to where logs were originally positioned, not directly underneath the removed log. After collecting a soil sample the hole was filled in with soil from the area to decrease effects of microtopography and a marker was placed in the centre so the same area was not used for subsequent sampling. On 24 March 2013 one soil sample (collected using a cookie cutter 5 cm deep and 9 cm diameter) was collected from the immediate vicinity of the logs, removed logs and from their corresponding open space sites. This sample was sent to CSBP soil and plant laboratory (Western Australia) for determination of soil organic carbon, total nitrogen, nitrate nitrogen, ammonium nitrogen, available phosphorus, available potassium, sulphur, electrical conductivity, and pH. Further soil samples were collected in the same way and sent for the same analysis as described above, on 6 May 2013, 1 August 2013, 5 November 2013 and 22 May 2014. Other soil samples collected on 24 March 2013 and on 24 March 2014 were retained for seed extraction. Seed extraction was conducted as per Malone (1967) within the week post collection and a cut test was used to determine viability of seeds.

Formation of a patch

The Purpunda Paddock (3 km from the Two Mile paddock) was selected for this part of the study due to the abundance of fallen logs and the presence of a piosphere effect (see Heshmatti et al. 2002). The stocking rate in Purpunda Paddock was reduced throughout the experiment until September 2013 when stock was completely removed. We chose two distances from the watering point: 400 m and 2 km, respectively representing a heavily grazed situation and a good rangeland condition. In open spaces at both distances we introduced logs and artificial logs on 22 May 2011. Logs were obtained from standing dead trees; they were 2-3 m in length and 10-30 cm diameter with simple branching structure. We also introduced pieces of PVC pipe of 22.5 cm diameter and 2 m length with caps on the ends as structures physically equivalent to logs, but without producing effects such as nutrient and organic material leaching that could be produced by logs. Henceforth we refer to these PVC pipes as "artificial logs". At each distance we walked along an arc, maintaining the set distance from the watering point, and at random distances along the curved transect we deployed logs and artificial logs to open spaces. Before placing a log or artificial log we collected two soil samples (using a cookie cutter 5 cm deep and 9 cm diameter) approximately 50 cm apart and combined these for further analysis. The log or artificial log

was then placed over where samples had been collected. At each distance from the watering point, six logs and six artificial logs were introduced, half in a north-south orientation, and half in an east-west orientation. Slopes are minimal in the area, and orientation with respect to sunlight was considered more likely to affect patch characteristics

To assess any accumulation of soil nutrients associated with the introduction of logs and artificial logs, we collected a further two soil samples (as above) approximately 1 m apart along a randomly selected side of each log, as well as two samples in open spaces. We collected these samples precisely three years after the initial samples were collected (22 May 2014). All soil samples collected throughout the duration of the experiment were sent to CSBP soil and plant laboratory (Western Australia) for determination of soil organic carbon, total nitrogen, nitrate nitrogen, ammonium nitrogen, available phosphorus, available potassium, sulphur, electrical conductivity, and pH.

To determine if there were any changes to annual plant communities after logs and artificial logs were introduced, we harvested all annual plants next to the logs and in open spaces on 2 Sep 2013. At each log or artificial log we collected annual plants within a plot of 80 x 20 cm on both sides of the log and the same sized plot in an adjacent open space. Plants were counted, identified, oven dried and weighed to determine above-ground biomass.

Statistical analyses

Differences in soil temperature were determined using split plot one-way ANOVA (after log transformation of the data to equalise variances). To determine if soil dried at different rates after a rainfall event, data were log transformed and linear regressions were performed. Soil nutrient analyses were analysed using split plot one-way ANOVA (after data were log transformed to equalise variances). Seed bank differences were determined using split plot one-way ANOVA, total propagules and total viable seeds were log transformed for analysis. We used Jmp In 4 to conduct analyses of variance to asses any differences in annual plant communities three years after introducing logs and artificial logs. To assess any differences in soil nutrient contents three years after introducing logs year we conducted split plot two-way ANOVA in Graph Pad Prism 6.

Results

Dissipation of a patch

Average maximum daily soil temperature was higher in open space soils than next to logs or, surprisingly, removed logs for June, July, August (winter in the southern hemisphere) and April while all other months showed a similar trend (fig 1). Average minimum daily soil temperature was higher next to logs than in the open for May, Jun, Jul, Aug, Dec and Apr. No difference in minimum temperatures was found between soils next to logs and removed logs, nor between open spaces and removed logs. These trends were consistent across all months.



Fig 1 Average maximum and minimum daily soil temperature at 5 cm depth for sites next to logs, open spaces and where logs were removed, encompassing April 2013 to April 2014 (* p < 0.1, ** p < 0.05, data log transformed for analysis, bars indicate SE- note that values are so low the symbols often obscure SE)

Soil volumetric water content was generally higher in soils in open spaces than soils next to logs or removed logs (fig 2a). When a single rainfall event (of 23.8 mm) and subsequent drying was analysed, open space soil had a significantly different slope, showing soil dried more slowly than next to log and removed log soils (fig 2b, p < 0.0001). Soils next to logs and removed logs dried at the same rate, but the water content of soils next to logs was

consistently higher than for soils next to removed logs (fig 2b, p < 0.0001, data log transformed for analysis).



Fig 2 Soil volumetric water content at 5 cm depth for log, open and removed log a) hourly between 24 Mar 2013 and 22 May 2014 (bracket indicates rainfall used for b) and b) immediately following a single rainfall event of 23.8 mm on Feb 13 2014 and subsequent drying

Soil nutrient analyses showed no significant effect of the removal of logs. Organic carbon (fig 3a) and total nitrogen (fig 3b) contents were consistently lower in open spaces than next to logs or removed logs, but no significant differences were found between logs and removed logs at any time. No significant differences were detected for any other nutrient across the three treatments.



Fig 3 a) organic carbon and b) total nitrogen contents in soils collected next to logs, removed logs and in open spaces periodically over 422 days (** p < 0.05, *** p < 0.01, ****p < 0.001, data log transformed for analysis, bars indicate SE)

No difference in the soil seed bank variables was ever detected between logs and removed logs but sites corresponding to these two treatments had consistently higher seed bank parameters than open space sites (fig 4). These results were expected in 2013, as logs had not yet been removed, but we did expect some change in 2014. The number of propagules was higher next to logs and removed logs than open spaces in 2013 and 2014 (figs 4a and 4b, p = 0.0013 and p < 0.0001 respectively). Propagule species richness was also higher next to logs and removed logs than in open spaces in both years (figs 4c and 4d, p = 0.0004 and p = 0.0008 respectively). Viable seed numbers were higher next to logs and removed logs than in open spaces (figs 4e and 4f, p = 0.0098 and 0.0005 respectively) and, similarly, viable seed species richness was higher next to logs and removed logs than in open spaces (figs 4g and 4h, p = 0.0020 and p = 0.0019 respectively).



Fig 4 a and b) Propagule numbers, c and d) propagule species richness, e and f) viable seed numbers and g and h) viable seed species richness, for 2013 (prior to log removal) and 2014 (one year post log removal) (split plot one-way ANOVA, bars indicate SE)

Formation of a patch

We did find some changes in soil nutrient contents, but not in the direction we expected. No difference was detected between introduced log and open soils for organic carbon in 2014, but soil collected in 2014 had significantly higher organic carbon contents than soil collected in 2011 (fig 5a, p = 0.0001). We similarly found no difference in log and open space soils in 2014 for all soil nutrient contents. We did find initial soils to have higher total nitrogen, available phosphorus and available potassium than log and open space soils collected in 2014 (figs 5b, 5c and 5d, p < 0.0001, p = 0.0151 and p = 0.0143 respectively). We also found that regardless of log or open site, organic carbon contents of soils were higher in the good condition area than in the degraded area (fig 6, p = 0.0254). No effect of introducing logs or pipes to the ground was found on annual plants after three years. We detected no effect for analyses using plant number, species richness or biomass when looking at log, artificial log or open, pristine or degraded, and orientation.



Fig 5 a) organic carbon, b) total nitrogen, c) available phosphorus and d) available potassium contents of initial soil samples in open spaces, and for post log deployment at open spaces and next to introduced logs (split plot two-way ANOVA, bars indicate SE)



Fig 6 organic carbon contents of soils in high and low grazing areas (split plot two-way ANOVA, bars indicate SE)

Discussion

Dissipation

Results from our patch dissipation experiment indicated that removing a fallen log did not immediately change levels of materials accumulated around logs and, surprisingly, that the temperature microclimate conditions associated with fallen logs were not affected by the removal of the log during the study period. The water dynamics, on the other hand, were changed: patches with logs removed retained less water and lost it faster than patches around logs.

Fallen logs have a moderating effect on soil temperatures with lower maxima and higher temperature minima compared with open spaces. This moderating effect is similar to that found associated with shading created by shrubs in arid systems (Segoli *et al.* 2012). Interestingly, the removal of fallen logs appeared to have only a very small immediate effect on this moderation: while maximum soil temperatures remained lower in removed log patches than in open spaces, no difference was detected for minimum soil temperatures between log and removed log soil or between removed log and open space soils. We did observe that there were abundant annual plants next to logs and removed logs over winter but not in the open, which may explain the reduction in maximum temperature, particularly during winter months, where logs were removed (A. Bowman personal observation).

While removing the logs only had minimum effect on soil temperature, the changes to soil volumetric water content were quite substantial. While log and removed log soil patches were consistently drier than open space soil, we had predicted that removing logs would trigger

changes making the patch more similar to open space soils. This was certainly not the case; instead soil volumetric water content was even lower in removed log patches. We suggest that the presence of logs can have two opposing effects on water infiltration: on the one hand they may change the surface of the soil in ways that reduce infiltration, most likely by creating a hydrophobic surface (e.g. because of organic matter properties or presence of a dense biophytic crust). On the other hand, during a rainfall event that triggers rainfall runoff, the physical presence of the log results in pooled water on the surface which will slowly infiltrate, increasing soil water content. Indeed structures such as logs on the ground obstruct runoff from open spaces and can favour infiltration (Ludwig *et al.* 2005). After removing a fallen log, surface soil properties could still reduce infiltration, but as there is no physical barrier to cause pooling, the microsite of the removed log ends up with even lower water content than the soil in the log patch.

Changes to microclimate conditions when a log is removed may be particularly important for germination and soil seed bank dynamics. There is evidence that higher soil temperatures can decrease seed viability and compromise bet-hedging strategies (Ooi 2012). We would expect that the moderating effect that logs have on soil temperatures create more favourable conditions for soil seed bank persistence than open spaces, and removing fallen logs would also reduce how favourable the environment is for seeds. Additionally, while seed dormancy for most species in this system is controlled by soil temperature (Facelli *et al.* 2005), germination success is generally determined by moisture (Baskin & Baskin 2014) and our findings show that removing a log would seem particularly unfavourable for seedling germination. Yet despite these speculations, we did not find any changes in the soil seed bank one year after removing fallen logs.

As expected we found no difference between log and removed log soil seed banks in 2013, as samples were taken prior to log removal, hence in 2013 removed log treatments were simply log treatments. Similar to Bowman *et al.* (in press) we found stark differences in the number and species richness of seeds between log and open space soils. Kinloch and Friedel (2005) also found lower seed densities associated with bare soil surfaces compared to areas with vegetation or depressions. However, we did expect that there would be some changes to the soil seed bank one year post log removal, as we expected the balance between germination, longevity and accumulation/removal would change, but this was not the case. The lack of change when a log is removed may simply be due to most species forming the soil seed bank

in Australian arid lands having small and variable germination fractions, resulting in little fluctuation in seed bank size (Ellner 1985; Pake & Venable 1996). However, Facelli *et al.* (2005) reported changes in soil seed bank composition over 18 months, but the dynamics was strongly species specific. Several species at our field site are known to have long persistence in the seed bank, with half-life estimated between 5-10 years, which is important during times unfavourable for germination and seed production (Facelli *et al.* 2005; Kinloch & Friedel 2005).

We did not find any changes in soil nutrient contents between log and removed log soils. This is consistent with previous studies that found soil nutrients in patches to take several years to dissipate. Bechtold and Inouye (2007) found the contrast in soil nutrients between shrub and open spaces decreased six years after they removed the canopy of the shrub, and Tiedemann and Klemmedson (1986) found similar changes, but 13 years after canopy removal. Facelli and Brock (2000) looked into the dissipation of soil nutrients after the death of a long lived tree, and they found soil nutrients remained higher than open space soils for at least 50 years. Additionally, we expect if grazing had been present during the study the patch may have dissipated at a faster rate through increased surface erosion where logs had been removed, but not next to logs as sheep avoid obstacles in the landscape (Lange 1969).

Formation of a patch

We were surprised to find that introducing logs to open spaces had no effect on soil nutrient contents or annual plant growth after three years. In our previous work we found changes in annual plant diversity after introducing logs to the same paddock after only four months (Bowman & Facelli 2013). Similarly, Tongway and Ludwig (1996) introduced piles of branches to the ground for three years and they found clear increases in soil carbon and nitrogen contents, as well as improved water infiltration rates and promotion of growth and establishment of perennial grasses (Ludwig & Tongway 1996).

The overall changes in soil nutrients over the three year period of the study were most unexpected. Rather than finding any changes produced by introducing logs, we found that soil contents of carbon, nitrogen, phosphorus and potassium all changed over a relatively short time. We suggest that changes to the grazing regime strongly affected soil nutrient contents in our accumulation experiment. The stocking rate in Purpunda Paddock was reduced throughout the experiment until September 2013 when stock were completely removed. However, current literature suggests that changes to soil properties after destocking are quite slow (Lesschen *et al.* 2008), and studies with grazing exclusion found organic carbon, total nitrogen and total phosphorus in soils all increased over time (Rong *et al.* 2014), while in our study only organic carbon increased, while other elements declined.

Conclusions

Our findings show patch formation and dissipation to be more complex than originally anticipated. Patch accumulation did not occur within a three year period, yet logs are known to create patches at twelve years in situ (Bowman et al. in press), suggesting that a log patch develops roughly between three and twelve years. After removing a log we found immediate changes to soil microclimate, but soil seed bank and soil nutrients continued to persist unchanged for at least one year. Given that our site had little topographic gradient, few large rainfall events (none of them torrential) and low or no grazing present, we are not surprised that soil nutrients and seed bank were unchanged. We predict that faster rates of dissipation will be found from removed patches in areas with greater topographic gradient and higher stocking rates. Our changes in microclimate conditions were highly unexpected, particularly regarding soil volumetric water content. The removal of a fallen log creates a patch that is unique in the environment and very different to any others in the system, as areas of log removal still retain some properties of the patch, but develop some new ones. More information is needed on the role of this patch type and about its length of its persistence. Given other patch types take several years to dissipate it is important to continue to monitor how this patch type changes with time. The dynamics of formation and dissipation of patches depend on the patch forming entity, yet there are still many questions unanswered about the dynamics of patchiness. Given the prevalence of grazing in arid lands this remains an important area for future research, as fallen logs are a patch forming entity which assist in the preservation of Australian flora in degraded arid systems. Ultimately a general model of patch formation and dissipation in arid lands is required for enhancing our ability to manage and restore these fragile ecosystems.

References

Barnes, P & Archer, S (1996) Influence of an overstorey tree (Prosopis glandulosa) on associated shrubs in a savanna parkland: implications for patch dynamics. *Oecologia* **105**: 493-500.

Baskin, CC & Baskin, JM (2014) Germination Ecology of Seeds in the Persistent Seed Bank. In 'Seeds (Second Edition).' (Eds CC Baskin and JM Baskin) pp. 187-276. (Academic Press: San Diego)

Bechtold, HA & Inouye, RS (2007) Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. *Journal of Arid Environments* **71**: 122-132.

Bowman, AS & Facelli, JM (2013) Fallen logs as sources of patchiness in chenopod shrublands of South Australia. *Journal of Arid Environments* **97**: 66-72.

Bowman, AS, Facelli, JM & Sinclair, R (in press) Long-term influence of fallen logs on patch formation and their effects under contrasting grazing regimes. *Austral Ecology*: n/a-n/a.

Callaway, RM, Nadkarni, NM & Mahall, BE (1991) Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* **72**: 1484-1499.

Crocker, RL (1946) An introduction to the soils and vegetation of Eyre Peninsula, South Australia. *Transactions of the Royal Society of South Australia* **70**: 83-105.

Ellner, S (1985) ESS germination strategies in randomly varying environments. I. Logistictype models. *Theoretical Population Biology* **28**: 50-79.

Facelli, J & Pickett, SA (1991) Plant litter: Its dynamics and effects on plant community structure. *The Botanical Review* **57**: 1-32.

Facelli, JM & Brock, DJ (2000) Patch dynamics in arid lands: Localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of South Australia. *Ecography* **23**: 479-491.

Facelli, JM, Chesson, P & Barnes, N (2005) Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. *Ecology* **86**: 2998-3006.

Facelli, JM & Temby, AM (2002) Multiple effects of shrubs on annual plant communities in arid lands of South Australia. *Austral Ecology* **27**: 422-432.

Friedel, MH, Sparrow, AD, Kinloch, JE & Tongway, DJ (2003) Degradation and recovery processes in arid grazing lands of central Australia. Part 2: vegetation. *Journal of Arid Environments* **55**: 327-348.

Heshmatti, GA, Facelli, JM & Conran, JG (2002) The piosphere revisited: plant species patterns close to waterpoints in small, fenced paddocks in chenopod shrublands of South Australia. *Journal of Arid Environments* **51**: 547-560.

Horton, JL & Hart, SC (1998) Hydraulic lift: a potentially important ecosystem process. *Trends in Ecology & Evolution* **13**: 232-235.

James, AI, Eldridge, DJ & Hill, BM (2009) Foraging animals create fertile patches in an Australian desert shrubland. *Ecography* **32**: 723-732.

Kinloch, JE & Friedel, MH (2005) Soil seed reserves in arid grazing lands of central Australia. Part 2: availability of 'safe sites'. *Journal of Arid Environments* **60**: 163-185.

Lange, RT (1969) The piosphere: sheep track and dung patterns. *Journal of Range Management* 22: 396-400.

Lesschen, JP, Cammeraat, LH, Kooijman, AM & van Wesemael, B (2008) Development of spatial heterogeneity in vegetation and soil properties after land abandonment in a semi-arid ecosystem. *Journal of Arid Environments* **72**: 2082-2092.

Ludwig, JA & Tongway, DJ (1996) Rehabilitation of semiarid landscapes in Australia. II. Restoring vegetation patches. *Restoration Ecology* **4**: 398-406.

Ludwig, JA, Wilcox, BP, Breshears, DD, Tongway, DJ & Imeson, AC (2005) Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* **86**: 288-297.

Malone, CR (1967) A rapid method for enumeration of viable seeds in soil. *Weeds* **15**: 381-382.

Noy-Meir, I (1985) Desert ecosystem structure and function. In 'Ecosystems of the World: Hot deserts and arid shrublands. Vol. 12A.' (Eds M Evenari, I Noy-Meir and DW Goodall) pp. 93-101. (Elsevier Science Publishers: Amsterdam)

Ooi, MKJ (2012) Seed bank persistence and climate change. *Seed Science Research* 22: S53-S60.

Pake, CE & Venable, DL (1996) Seed banks in desert annuals: Implications for persistence and coexistence in variable environments. *Ecology* **77**: 1427-1435.

Popp, A, Blaum, N & Jeltsch, F (2009) Ecohydrological feedback mechanisms in arid rangelands: Simulating the impacts of topography and land use. *Basic and Applied Ecology* **10**: 319-329.

Reid, KD, Wilcox, BP, Breshears, DD & MacDonald, L (1999) Runoff and erosion in a Piñon–Juniper woodland influence of vegetation patches. *Soil Sci. Soc. Am. J.* **63**: 1869-1879.

Rong, Y, Yuan, F & Ma, L (2014) Effectiveness of exclosures for restoring soils and vegetation degraded by overgrazing in the Junggar Basin, China. *Grassland Science* **60**: 118-124.

Sala, OE, Golluscio, RA, Lauenroth, WK & Soriano, A (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* **81**: 501-505.

Segoli, M, Ungar, ED & Shachak, M (2012) Fine-scale spatial heterogeneity of resource modulation in semi-arid "islands of fertility". *Arid Land Research and Management* **26**: 344-354.

Sinclair, R (2005) Long-term changes in vegetation, gradual and episodic, on the TGB Osborn Vegetation Reserve, Koonamore, South Australia (1926-2002). *Australian Journal of Botany* **53**: 283-296.

Sparrow, AD, Friedel, MH & Tongway, DJ (2003) Degradation and recovery processes in arid grazing lands of central Australia Part 3: implications at landscape scale. *Journal of Arid Environments* **55**: 349-360.

Thompson, S, Assouline, S, Chen, L, Trahktenbrot, A, Svoray, T & Katul, G (2014) Secondary dispersal driven by overland flow in drylands: Review and mechanistic model development. *Movement Ecology* **2**: 7.

Tiedemann, AR & Klemmedson, JO (1986) Long-term effects of mesquite removal on soil characteristics: I. nutrients and bulk density. *Soil Sci. Soc. Am. J.* **50**: 472-475.

Tongway, DJ & Ludwig, JA (1994) Small-scale resource heterogeneity in semi-arid landscapes. *Pacific Conservation Biology* **1**: 201-208.

Tongway, DJ & Ludwig, JA (1996) Rehabilitation of semiarid landscapes in Australia. I. Restoring productive soil patches. *Restoration Ecology* **4**: 388-397.

Tongway, DJ, Ludwig, JA & Whitford, WG (1989) Mulga log mounds: Fertile patches in the semi-arid woodlands of eastern Australia. *Austral Ecology* **14**: 263-268.

Vázquez, DP, Alvarez, JA, Debandi, G, Aranibar, JN & Villagra, PE (2011) Ecological consequences of dead wood extraction in an arid ecosystem. *Basic and Applied Ecology* **12**: 722-732.