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Decade-long response of arid-land mallee vegetation to fire, flooding and grazing in south-eastern Australia

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ABSTRACT

Australian arid vegetation has evolved within highly variable environments characterised by low rainfall and sporadic fire events. Episodic high rainfall events are a significant factor in plant species recruitment, but their unpredictability makes them difficult to study. We report on the response of vascular plants to a major rainfall event and flood in an arid region of south-eastern Australia. Fire that occurred two months before the flood was incorporated into the study. Paired fenced and unfenced plots were established at control locations and also in areas that had been either flooded, burnt, or flooded and burnt. Objectives were to quantify the long-term effects of fire, flood and vertebrate herbivory, and their interactions, on vegetation composition, plant life forms and species diversity. We found that relative to controls (i) there was a significant effect of flooding on vegetation composition, (ii) changes in life form abundance were driven by flooding and grazing, (iii) there was a strong positive relationship between grazer exclusion and species diversity that was maintained over time and (iv) there was little effect of fire. Understanding the long-term effects of both natural disturbances and vertebrate herbivory will benefit plant conservation in the arid zone.

Keywords: disturbance: Mallee; Principal Response Curve: recovery; arid; succession; weed

1. Introduction

Over the past century several biophysical and human-induced factors have played their roles in the spatial and temporal development of vegetation structure and composition globally (Stenseth et al., 2002). In arid environments climate, in particular, has determined vegetation community structure, function, and patterns of species colonization and succession (Westbrooke et al., 2005; Thibault and Brown, 2008). For example, water availability plays a substantial role in the germination and development of arid zone trees such as *Casuarina pauper*, *Alectryon oleifolius* and *Callitris verrucosa* (Westbrooke, 1998), and even minor rainfall events (of 5 mm or less) may affect the development of some herbaceous species (Sala et al., 1988).

Rainfall events are often spatially patchy; some areas receive substantial rain with adjacent areas receiving none. While flooding is uncommon in the arid zone, except in watercourses and local depressions, the flat topography of much of the Australian landscape, combined with the influence of the El Niño-Southern Oscillation, suggests that substantial areas of desert vegetation may be submerged occasionally. For example, the Lake Eyre Basin in South Australia is subject to periodic flooding, substantially altering the state of the local ecosystem (Williams, 1970). In the context of vegetation, sustained inundation will kill many species, but also create space for regeneration from seeds as the floodwaters subside (Westbrooke et al. 2005). Further, mass movement of water resulting from flooding is likely to introduce seeds from other areas. This may be an important form of dispersal for some arid zone species (Kehr, et al., 2014) but can also facilitate the introduction of exotics into the plant community (Griffin et al., 1989; Florentine et al., 2006). Additional factors influencing plant communities in the Australian arid zone include fire and herbivory (Westbrooke et al., 2005). Fire is a common occurrence in arid landscapes, and has both short- and long-term effects. Depending on its intensity, fire may remove or kill above-ground plant parts, thus altering the physiognomy of vegetation as well as its composition (Bradstock 2008). As a result, arid zone species have developed various mechanisms to ensure their survival in the face of periodic burning. Mallee eucalypts, for example, will regrow after fire from underground lignotubers (Specht, 1981). However, fire in mallee vegetation will also consume much of the available seed, with differing mortality among species (Steers and Allen, 2012).

In addition to fire, grazing and browsing by both native and introduced vertebrate herbivores is widespread in Australia's arid zone and significantly affects species composition as well as the overall physiognomy of the vegetation (Landsberg et al., 2003). Selection for palatable forage will likely impact some plant species more than others, while high grazing pressure may result in a substantial reduction in plant biomass as a whole (Lange 1969; Castellano and Valone, 2006). Additionally, trampling by introduced vertebrate such as goats and cattles, particularly around focal points in the landscape such as water points or areas of palatable vegetation, can lead to compaction and subsequent loss of soil structure (Tongway et al., 2003).

The effects of fire (Hodgkinson and Oxley 1990; Hill and French, 2004), climate (Holmgren et al., 2001; Stenseth, et al., 2002), and grazing (Lange 1969; Landsberg et al., 2003; D'Souza et al., 2013) on arid zone vegetation have been the subject of considerable research. Such research was often under partially controlled conditions and has yielded

important information for the management of the large grazing properties often established in arid environments.

Although the influence of flooding on Australian arid zone vegetation has been studied previously, existing work has reported short-term effects (Wardle et al. 2013; D'Souza et al., 2013). Further, no studies have examined the effect of flooding in combination with other potential drivers of vegetation succession such as fire and herbivory. A fire in the arid zone of southeastern Australia in December 1996, followed by a flood event in 1997, provided a rare opportunity to study the independent and combined effect of these factors on the recovery of the local vegetation. Further, the establishment of exclusion plots in both flooded and burnt areas enabled the influence of vertebrate herbivory to be quantified. In this paper, we report 11 years of monitoring data describing the response of vascular plants to different combinations of flood, fire and grazing. Specifically, we describe temporal patterns in (i) vegetation composition (ii) life-form density and (iii) species diversity.

2. Material and Methods

2.1. Study area

Nagaella Station is located in south western New South Wales, Australia, approximately 120 km southwest of Broken Hill, close to the South Australian border (Electronic appendix). The landscape is dominated by a system of linear dunes and swales orientated west to east (Walker, 1991). Most of the land area is < 100 m above mean sea level. The dunes generally have a poorly developed soil profile of deep calcareous sands with high water infiltration, and concomitant low levels of run-off (Lawrie and Stanley, 1980). It is likely that the dunes may have accumulated in stages to their present height of up to 12 m above the swales. The lower-lying swales are up to 500 m wide with isolated flats and depressions of soils with heavier texture (Walker, 1991), and occasional copi (gypsum) rises. The heavier soils in this landscape result in a higher run-off. The region is subject to a severe moisture deficit, with annual rainfall averaging between 200 and 300 mm and potential annual evaporation of around 2000 to 2400 mm (Australian Bureau of Meteorology 2012). Generally, summer temperatures are high (February mean daily max = 32° C; min = 16° C) and winter mild (July mean daily max = 15° C; min = 5° C) (Australian Bureau of Meteorology 2012). Average annual rainfall (mm) and average minimum and maximum temperatures for the data collection period are given in Fig. 1.

The vegetation of the study area is predominantly eucalypt shrubland (mallee) dominated by *Eucalyptus gracilis*, *E. dumosa*, *E. oleosa* and *E. socialis*. Other vegetation in the region include *Atriplex vesicaria* (Bladder Saltbush), *Halosarcia* sp. *Frankenia* sp. *Osteocarpum* sp. in low open shrubland, and *Dodonaea viscosa* ssp. *angustissima* and *Eremophila sturtii* in shrubland conditions (Westbrooke et al., 1998). The region was one of the last to be opened up for pastoral farming (1928), primarily due to the very low productivity of palatable plants (Lawrie and Stanley, 1980), and a lack of a reliable water supply. Fires occur periodically with the size of affected areas generally less than 10,000 ha in extent. The last fire recorded for the study site occurred in the December 1996 (Westbrooke et al., 2005). Whilst it is known that fire events play a vital role in the ecology of arid zone vegetation, the natural fire frequency of mallee vegetation is poorly understood as much of the area has been significantly disturbed by agricultural activity since the 1880s. As a consequence, many areas have been influenced by past grazing and unplanned fire of human origin. Historical

fire intervals in mallee-type vegetation may be approximately 65 years, and characteristics of individual fires are highly influenced by factors such as weather and fuel age (O'Donnell et al. 2011).

2.2. Grazing history of Nagaella station (1999 to 2011)

Nagaella was first taken up as a pastoral property in 1928 following subdivision of the large Lake Victoria lease (Westbrooke, 2012). From that time until the mid-1990s it was subject to grazing by Merino sheep (*Ovis aries*) at a stocking rate of around 0.1 per ha. From the mid-1990s, and throughout the study reported here, it was grazed by feral goats under a low intensity husbandry management program. Absolute stocking rates of goats are difficult to determine, but based on discussion with managers and limited monitoring, it appears to have been between 0.1 and 0.4 per ha. In addition to the stock, there are populations of native kangaroos: *Macropus fuliginosus melanops* (Western Grey Kangaroo) and *Macropus rufus* (Red Kangaroo). *Macropus fuliginosus* tend to be resident in an area whereas *M. rufus* are transient and move large distances according to seasonal conditions and thus overall population density fluctuate. Based on transect surveys, the density of the two species combined ranged from 0.02 - 0.05 individuals per ha (unpublished data). During the 2002–2004 vegetation sampling period, small numbers of *Oryctolagus cuniculus* (rabbits) were evident while during the last five years of our study (2005 – 2010) there was no evidence of rabbits in the study area.

2.3. Sequence of events and previous research

Of particular importance to this study was the wildfire in December 1996, which burnt across Nagaella Station, in part extending over the area that was subsequently flooded. In February 1997, a rainfall event of 200 mm within a 24 h period resulted in major flooding within the Olary Creek catchment of arid South Australia and New South Wales. The southern channel of Olary Creek washed through an area of mallee vegetation to form a transient lake on Nagaella station. The lake covered a surface area of around 300 ha to a depth of up to 2 m and remained flooded for approximately a year and a half. Rainfall records collected from Olary and Mannahill stations, adjacent to the main catchment of Olary Creek (Clewett et al., 2003), indicate that similar flood events may have occurred in 1921, 1950, and 1989 (Westbrooke and Florentine 2005, Morton et al., 2011).

In February 1999, paired grazing enclosure plots (see details below) were established in areas that had been subjected to different combination of fire and flood, to facilitate an additional comparison of vegetation recovery under grazed and ungrazed conditions. Each pair consisted of an enclosure that prevented grazing by vertebrates such as rabbits, kangaroos, sheep, and goats, and an open adjacent area that did not exclude these species. Westbrooke et al. (2005) reported on short-term vegetation responses in these plots. Although flood and fire triggered the germination and recruitment native species, the number of plant species per plot decreased from 11.8 ± 2.16 (mean \pm SE) in 1999 to 5.7 ± 0.79 in 2002, and species composition was affected by grazing. Other reports on the short-term responses showed that the flooding and fire events created an opportunity for exotic species to invade (Westbrooke et al., 2005; Florentine et al., 2006).

2.4. Plot establishment and vegetation survey

To assess the relative impact of flood, fire and grazing, a long-term study was conducted in and around the newly formed lake on Nagaella Station. Permanent 625 m² (25 m x 25 m) plots were established in September 1999, following flood and fire events in 1997 and 1996, respectively. The permanently marked plots were placed in pairs (Electronic appendix) in areas that had one of the following histories: (i) neither flooded nor burnt, which we subsequently refer to as the control (n = 2), (ii) flooded only (n = 4); (iii) burnt only (n = 2); and (iv) flooded and burnt (n = 2). In all cases, one plot in each pair was fenced to exclude kangaroos, feral goats, sheep and rabbits. The other was established immediately adjacent to the first, but unfenced to permit grazing. The fence consisted of 1.7 m tall, 15 cm mesh overlaid with 5 cm mesh rabbit wire. Each plot was subdivided into 5 m x 5 m subplots with their corners permanently marked using aluminium pickets to facilitate more precise documentation of the vegetation. In each plot, the number of individuals of every plant species was recorded in September 1999; October 2002, 2003, and 2004, July 2005, October 2006, September 2007, 2008, February 2010, April 2011, and February 2012. Species that formed clear individuals (ramets) were counted individually. For some species where counting the number of ramets was practically impossible, the number of hummocks were counted instead (e.g. larger *Triodia scariosa*). Similarly, multi-stemmed mallees were counted as genets, not as number of stems.

Our study was set up opportunistically to take advantage of two disturbance events (fire and flood) that occurred in the same location. As such, it has several limitations that influence the interpretation of results. First, we sampled a single fire and flood event, thus direct spatial extrapolation of our results is inappropriate. Second, due to time and financial constraints, the number of replicate plots within each sampled state was small, raising the possibility that parts of the data set are not representative of effects occurring in the study area. However, changes detected in the sampled plots were consistent with our observations of plant responses in other parts of the flooded and burnt landscape around Nagaella station. Consequently, we have analysed our data and interpreted the outputs assuming that our samples were representative of study-area wide effects. Third, the power of the statistical procedures we employed was likely low, again due to the small number of plots. Thus while our analyses was able to detect large effects, more subtle changes may have gone undetected.

2.5. Statistical analysis

We used Principal Response Curves (PRC; [van den Brink & ter Braak 1999](#)), in CANOCO 5 ([ter Braak and Šmilauer 2012](#)), to describe the temporal shifts in vegetation composition in response to flood, fire and grazing (data log (x+1) transformed). As fenced and unfenced plots were spatially nested, we ran independent PRCs for each of these data sets, testing for the effects of fire and flood at grazed and ungrazed states separately. The analysis proceeded in three stages. First we evaluated the statistical significance of the trends detected by the PRC. Second we re-ran the PRC with all available factors to facilitate the presentation and interpretation of observed patterns. Third, as fire had no detectable effect, we illustrated the effect of flooding by ignoring fire, thereby effectively doubling the sample size.

We summed the number of species per plot of each of the following life forms: monocarp, exotic, tussock, grass, herb, shrub or tree. Averages were then calculated separately for flood/non-flood and fenced/unfenced plots (ignoring fire). We defined tussock as a perennial, monocotyledonous plant (or the structural herbaceous equivalent) with long-lived linear leaves that arise from a narrow base that is much smaller in diameter ($< \text{half}$) than is the canopy or crown.

We used the raw data from all 104 species to calculate the geometric mean of species abundance. The geometric mean represents an index of species diversity that has several mathematical and statistical properties that make it superior to more frequently used indices such as those of Shannon and Simpson (Buckland et al., 2012; van Strien et al., 2012). The geometric mean will change to reflect changes in the actual abundance of species (positive or negative), even if their relative abundances are held constant. In contrast, the values of Shannon's and Simpson's index remain unchanged. As a consequence, the geometric mean forms the basis of several large-scale biodiversity measures, including the Living Planet Index (Loh et al., 2005). Because the geometric mean is undefined for values of zero, we replaced all zeros in the data set with 0.1 before calculating its value. To ensure that this choice did not produce a spurious result, we also trialled substitution of 0.01 and 0.001 for zero cases, but in all trials the resulting values of the index were strongly correlated ($r \geq 0.96$).

The response of species diversity to disturbance and grazer exclusion over time was analysed using a generalized additive mixed model (GAMM) assuming a Gaussian error distribution. We used a mixed model to account for spatial and temporal nesting in the data, specifying the random effect as year|plot, and applied this within a generalised additive framework to model the non-linear patterns that were apparent in the raw data. In addition to standard parametric coefficients, generalized additive models incorporate non-parametric smoothing functions to enable flexible modelling of non-linear responses, automatically determining an appropriate degree of smoothing using generalized cross validation (Wood, 2006). We built two models to examine the effect of (a) flooding and fire and (b) grazer exclusion (fenced and unfenced) on species diversity over time, using a varying-coefficient model to generate an independent smoothing function for each level of the categorical predictors. All models were run in the R statistical environment (R Core Team 2013) using the gamm4 package (Wood 2012). We used residual plots to test analytical assumptions, and identified one large outlier. However, we ran the final analyses on the complete data set as outlier exclusion had little effect on the output and did not alter interpretation.

3. Results

A total of 104 species from 31 plant families were recorded during the sampling period. Of those species recorded, 14.6% ($n = 15$) were exotic. The following life forms were identified: polycarp (55), monocarp (48), herbs (45), shrubs (13), tussock (6), hummock (1) and grasses (5). About 25% of all species were from the families Chenopodiaceae (26) and 16% from the Asteraceae.

3.1. Principal Response Curves

Initially we detected a significant difference in species composition of the vegetation due to the treatment history in fenced plots ($F = 55.7$; $P = 0.03$), but not in unfenced plots ($F =$

30.1; $P = 0.09$). Re-analysis of the full data set suggested that fire had no long-term impact: burnt plots closely tracked the control while burnt and flooded plots tracked those only flooded (Fig. 2). Species composition in the flooded plots diverged from non-flooded plots for 5-6 years, after which there was a tendency for vegetation to become more similar. The temporal trends were very similar in the fenced and un-fenced plots (Fig. 2a, b). As the previous step had shown that fire had no discernible effect, the PRCs were re-run contrasting only flood with control. In this case the maximum difference between flooded and non-flooded plots was observed after four years, after which vegetation composition became more similar over time (Fig. 3a, b).

The temporal trends were very similar in the fenced and un-fenced plots (Fig. 3a, b). Control plots were characterised by eucalypt trees, the sub-shrub *Sclerolaena parviflora*, shrubs *Eremophila* spp., the hummock forming *Triodia scariosa*, and the annual *Ptilotus exaltatus*. In contrast, flooded plots were characterised by native grasses (*Stipa* sp.), and non-native species: grasses (*Schismus barbatus*, *Bromus rubens*) a shrub (*Nicotiana glauca*) and herbs (*Spergularia rubra*, *Sonchus asper*).

3.2. Life form analysis

Relative to controls, flooding and grazing caused the largest changes in life form abundance. Flooding reduced the abundance of trees and shrubs, but only in grazed plots, with the largest reductions observed 7-11 years after the flood (Fig. 4 a,b,c,d,e and f). The increase in abundance of herbs, monocarps, grasses, and exotics, was most pronounced in fenced plots (Fig 4 b,c,d, and f). Initially there were fewer tussock grasses in flooded plots, but these regrew best when subjected to grazing (Fig. 4e).

3.3. Species diversity

Species diversity was strongly influenced by grazer exclusion (Table 1, Fig. 5). Over the 11 year sampling period, diversity remained constant in unfenced plots, but was substantially higher in fenced plots, showing a hump-shaped trend that peaked around eight years after fence construction. The response of species diversity to fire, flood and fire and flood was also hump-shaped and higher than control values, but did not differ statistically from controls ($P \geq 0.12$).

4. Discussion

Disturbances caused by high rainfall events influence vegetation community composition in the arid zone and elsewhere (Holmgren et al., 2001, Westbrooke et al., 2005), but due to their unpredictable nature such effects are rarely documented (Thibault and Brown, 2008). Further, existing research (Westbrooke et al., 2005; Westbrooke and Florentine, 2005; Travers and Eldridge, 2013) has presented short-term effects of flooding on arid zone vegetation. In this study we report how a major flood in the arid zone of southeastern Australia influenced vegetation composition, life-form density and species diversity over an 11 year period. Fire and vertebrate herbivory were also investigated as two additional factors that, either in isolation or in combination with flooding, may influence arid zone vegetation over the longer term.

4. 1. Vegetation responses: flooding

In arid environments, the successful recruitment of trees and other perennial plant species is confined to times when soil water is persistent enough to allow newly recruited seedlings to establish and survive (Nano and Pavey, 2013). Typically such events are created during consecutive years of high rainfall, but may also be as a result of flooding as described here. Flooding caused changes in species composition, and to the density of some life forms, but had no detectable effect on species diversity. Flooding of arid zone vegetation has been shown to alter species composition in the short-term by promoting the germination of early successional species. Our data were consistent with these findings as species composition in control and flooded plots differed substantially four to five years after the flood event. In subsequent years, however, the composition of control and flooded plots began to converge, although a substantial difference still existed at the end of the sampling period. These are the first data indicating that compositional changes in arid zone vegetation due to flooding may last well beyond a decade. Additional long-term data after other flood events are needed to confirm this finding.

The composition of species in the flooded plots was characterised by native grasses such as the various species of *Stipa*, including *S. drummondii*, *S. elegantissima* and *S. scabra*, as well as a number of non-native species, such as *Schismus barbatus*, *Bromus rubens*, *Spergularia rubra*, *Sonchus asper* and *Nicotiana glauca*. This is consistent with the life form analysis which showed that the density of monocarps, grasses and exotic species increased in flooded plots. Hence, an immediate, and possibly enduring, effect of flooding was the invasion of short-lived grass species and the invasive shrub *N. glauca*. We predict that subsequent floods will further disperse such species.

4.2. Vegetation responses: fire

Fire may affect vegetation dynamics in various ways (see Harrington *et al.* 1984, Trollope 1999), for instance by killing individual plants or parts of plants, or by stimulating recruitment from seeds or through vegetative regrowth. However, the December 1996 fire had no detectable effect on species composition or diversity in the decade-long follow up, although we note that any possible immediate post-fire flush of seedlings was not recorded. This lack of reaction was unexpected since existing research shows that fire does have an effect on vegetation in arid ecosystems (Hill and French 2004). We consider two possible explanations for this limited effect. Recruitment in the previously inundated areas might have overshadowed the removal of plants by fire. Alternatively, the intensity of the fire may have been low, reducing plant mortality and facilitating rapid return of the plant community to the pre-fire state.

4.3. Vegetation responses: grazing

Given the low density of rabbits during the study period (rabbit warrens were only observed during the early part of our study), the bulk of the herbivory must be attributed to feral goats and kangaroos. Grazing, or the absence thereof, by large herbivores affected species diversity over the eleven-year sampling period. Plots protected from grazing had higher diversity, mainly caused by higher species richness, with the average number of species detected in fenced plots amounting to twice that of unfenced plots (14.5 and 7.0 species per plot). Palatable species such as *Acacia aneura*, *A. burkittii*, *A. colletioides*, *A. ligulata*, *A.*

wilhelmiana, *Eutaxia microphylla*, *Maireana appressa*, *M. sedifolia*, *Senna artemisioides* and several annual species occurred more than twice as frequently in the fenced plots. Our results are consistent with other studies showing a substantial effect of vertebrate herbivory on vegetation composition in arid and semi-arid areas (Wesuls et al. 2012; Lawley et al., 2013).

4.4. Effects of flooding and grazing

We found that the flooding event reduced the abundance of trees and shrubs, but monocarps, exotics, herbs and grasses (Fig. 4 b,c,d,f) increased. In most cases, fenced plots had higher abundances of species than unfenced plots. It was observed that tussock-forming species occurred less frequently in flooded plots, but regrew best when plots were subjected to grazing (Fig. 4). The abundance of herbaceous plants may be attributable to various factors. We speculate that many of the seeds were introduced after the inundated areas had dried out, as the seed of previously resident plants would have died under prolonged water logging. Lighter grass seed would then be reintroduced by wind from the immediate surroundings, while heavier seed would require other vectors (Westbrooke and Florentine 2005; Florentine et al. 2006)

The response of the vegetation to the disturbances flood and fire, under continuously maintained grazing, showed different short- and long-term effects. During the first few years the vegetation developed within known boundaries that were identified by other studies. Towards the end of the reporting period, however, the composition of disturbed and undisturbed vegetation converged. Fire and flooding effects may thus have limited lifespans. Grazing, on the other hand, resulted in long-term modification of the vegetation, both in composition and physiognomy, and may be equally attributable to differences in grazing regimes between pre- and post- European times.

5. Conclusions

This study reports on the combined effects of fire, flooding and grazing on an arid-zone mallee community in south-western New South Wales. The initial response of the vegetation to flooding followed patterns similar to those established by other studies, but, in contrast to previous work, fire alone had no discernible effect. Eleven years after the flood vegetation composition in flooded plots differed from controls, and species diversity was greater in fenced compared to unfenced plots. Although the impact of flooding and grazing on vegetation peaked between six and 10 years after the flood, effects may last well beyond a decade. Further, flooding increased the abundance of exotic species, adding to the evidence that floods can facilitate the establishment of exotic plants in arid and semi-arid environments (Florentine et al. 2006).

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References

- Australian Bureau of Meteorology 2012. Climate, Australian Bureau of Meteorology, viewed 14 January 2012, <<http://www.bom.gov.au/climate>>.
- Bradstock, R.A., 2008. Effects of large fires on biodiversity in south-eastern Australia: disaster or template for diversity? *Int. J. Wildland Fire* 17, 809–822.
- Buckland, S.T., Baillie, S.R., Dick, J.M., Elston, D.A., Magurran, A.E., Scott, E.M., Smith, R.I., Somerfield, P.J., Studeny, A.C. Watt, A., 2012. How should regional biodiversity be monitored? *Environ. Ecol. Stat.* 19, 601–26.
- Castellano, M.J., Valone, T.J., 2006. Effects of livestock removal and perennial grass recovery on the lizards of a desertified arid grassland. *J. Arid Environ.* 66, 87–95
- Clewett, J.F., Smith, P.G., Parridge, D.A., George, D.A., Peacock, A., 2003. 'Australian Rainman: Rainfall Information for Better Management'. (Department of Primary Industries: Brisbane.).
- D'Souza, J.B., Whittington, A., Dickman, C.R., Leung, L.K.P. 2013, Perfect storm: Demographic responses of an irruptive desert mammal to prescribed burns following flooding rain. *Austral Ecol.* 38, 765–776.
- Eldridge, D.J., Val J. James, A.I., 2011. Abiotic effects predominate under prolonged livestock-induced disturbance. *Austral Ecol.* 36, 367–377.
- Florentine, S.K., Westbrooke, M.E., Gosney, K., Ambrose, G., 2006. The arid land invasive weed *Nicotiana glauca* R. Graham (Solanaceae): population and soil seed bank dynamics, seed germination patterns and seedling response to flood and drought. *J. Arid Environ.* 66, 218–230.
- Griffin, G. F., Smith, D.M.S., Morton, S.R., Allan, G.E., Masters, K.A., Preece, N. 1989. Status and implications of the invasion of tamarisk (*Tamarix aphylla*) on the Finke River, Northern Territory, Australia. *J. Environ. Manage.* 29, 297–315.
- Harrington, G.N., Friedel, M.H., Hodgkinson, K.C., Noble, J.C., 1984. Vegetation ecology and management. In Harrington, G.N., Wilson, A.D., Young, M.D., (Eds.), *Management of Australia's Rangelands*. CSIRO, Melbourne. pp 41–62.
- Hill, S.J., French, K., 2004. Potential impacts of fire and grazing in an endangered ecological community: plant composition and shrub eucalypt regeneration in Cumberland plain woodland. *Aust. J. Bot.* 52, 23–29.
- Hodgkinson, K.C., Oxley, R.E., 1990. Influence of fire and edaphic factors on germination of the arid zone shrubs *Acacia aneura*, *Cassia nemophila* and *Dodonaea viscosa*. *Aust. J. Bot.* 38, 269–279.
- Holmgren, M., Schelfer, M., Ezcurra, E., Gutierrez, J. R., Mohren, G.M.J., 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.* 16, 89–94.
- Kehr, J.M., Merritt, D.M. Strombergm, J.C. 2014. Linkages between primary seed dispersal, hydrochory and flood timing in a semi-arid region river. *J. Veg. Sci.* 25, 287–300.
- Landsberg, J., James, C.D., Morton, S.R., Muller, W.J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. *J. Appl. Ecol.* 40, 1008–1024.
- Lange, R.T., 1969. The Piosphere: Sheep track and dung patterns. *Rangeland J.* 22, 396–400.
- Lawley, V., Parrott, L., Lewis, M., Sinclair, R., Ostendorf, B., 2013. Self-organization and complex dynamics of regenerating vegetation in an arid ecosystem: 82 years of recovery after grazing. *J. Arid. Environ.* 88, 156–164.
- Lawrie, J.W., Stanley, R.J., 1980. Representative land systems of the mallee lands in the Western Division of NSW. In Storrier, R.R., Stannard, M.E., (Eds.), *Aeolian landscapes*

- in the semi-arid zone of south eastern Australia. Australian Society of Soil Science - Riverina Branch, Wagga Wagga.
- Loh, J., Green, R.E., Ricketts, T., Lamoreux, J., Jenkins, M., Kapos, V., Randers, J., 2005. The Living Planet Index: using species population time series to track trends in biodiversity. *Phil. Trans. R. Soc. B – Biol. Sci.* 360, 289–95.
- Morton, S.R., Smith, D.M.S., Dickman, C.R., Dunkerley, D.L., Friedel, M.H., McAllister, R.R.J., Reid, J.R.W., Roshier, D.A., Smith, M.A., Walsh, F.J., Wardle, G.M., Watson, I.W., Westoby, M. 2011. A fresh framework for the ecology of arid Australia. *J. Arid Environ.* 75, 313–329.
- Nano, C.E.M., Pavey, C.R., 2013. Refining the ‘pulse-reserve’ model for arid central Australia: Seasonal rainfall, soil moisture and plant productivity in sand ridge and stony plain habitats of the Simpson Desert. *Austral Ecol.* 38, 741–753.
- O’Donnell, A.J., Boer, M.M., McCaw, W.L., Grierson, P.F., 2011. Vegetation and landscape connectivity control wildfire intervals in unmanaged semi-arid shrublands and woodlands in Australia. *J. Biogeogr.* 38, 112–124.
- R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, Retrieved from <http://www.R-project.org>
- Sala, O.E., Parton, W.J., Joyce, L.A., Lauenroth, W.K., 1988. Primary production of the central grassland region of the United States. *Ecology* 69, 40–45.
- Specht, R.L., 1981. Mallee ecosystems in South Australia. Mediterranean-type shrublands. In Di Castri, F., Goodall, D. W., Specht, R. L., (Eds.), Elsevier North Holland. Amsterdam. pp. 203–231.
- Steers, R.J., Allen, E.B., 2012. Impact of recurrent fire on annual plants: a case study from the western edge of the Colorado desert. *Madrono* 59, 14–24.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K., Lima, M., 2002. Ecological effects of climate fluctuations. *Science* 297, 1292–296.
- ter Braak C.J. F., Šmilauer, P., 2012. Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power, Ithaca, USA, 496 pp.
- Thibault, K.M., Brown, J.H., 2008. Impact of an extreme climatic event on community assemblage. *Proc. Natl. Acad. Sci. USA* 105, 3410–3415.
- Tongway, D.J., Sparrow, A.D., Friedel, M.H., 2003. Degradation and recovery process in arid grazing lands of Central Australia Part 1: soil and land resources. *J. Arid Environ.* 55, 301–326.
- Travers, S.K., Eldridge, D.J., 2013. Increased rainfall frequency triggers an increase in litter fall rates of reproductive structures in an arid eucalypt woodland. *Austral Ecol.* 38, 820–830.
- Trollope, W.S.W., 1999. Veld Burning. In Tainton, N., (Ed.), *Veld Management in South Africa*. University of Natal Press, Pietermaritzburg, South Africa. pp 217–245
- van den Brink, P.J., ter Braak, C.J.F., 1999. Principal response curves: Analysis of time dependent multivariate responses of biological community to stress. *Environ. Toxicol. Chem.* 18, 138–148.
- van Strien, A.J., Soldaat, L.L., Gregory, R.D., 2012. Desirable mathematical properties of indicators for biodiversity change. *Ecol. Indicators* 14, 202–208.
- Walker, P.J., 1991. Land Systems of Western New South Wales. In Technical Report, 25: Soil Conservation Service of New South Wales.
- Wardle, G.M., Pavey, C.R., Dickman, C.R. 2013. Greening of arid Australia: New insights from extreme years. *Austral Ecol.* 38, 731–740.
- Westbrooke, M.E., Florentine, S.K., 2005. Rainfall-driven episodic flood events: Are they a major factor in moulding Australian arid land vegetation patterns? *Aust. Geogr.* 36, 171–181.
- Westbrooke, M.E., Florentine, S.K., Milberg, P., 2005. Arid land vegetation dynamics after a rare flooding event: influence of fire and grazing. *J. Arid Environ.* 61, 249–260.

- Westbrooke, M., 2012. The pastoral history, biological and cultural significance of the Scotia Country, far western New South Wales. *Proc. Linnean Soc. New South Wales* 134, 55–68.
- Westbrooke, M.E. 1998. The Ecology and Regeneration Status of Belah Woodland in Southeastern Australia. (PhD Thesis), La Trobe University, Victoria.
- Westbrooke, M.E., Miller, J.D., Kerr, M.K.C., 1998. Vegetation of the Scotia 1:100,000 map sheet, western New South Wales. *Cunninghamia* 5, 665–684.
- Wesuls, D., Oldeland, J., Dray, S., 2012. Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach. *J. Veg. Sci.* 23, 98–113.
- Williams, G.E., 1970. The central Australian stream floods of February-March 1967. *J. Hydrol.* 11, 185–200.
- Wood, S.N., (2006) *Generalized Additive Models: An Introduction with R*. Chapman and Hall /CRC Press, Boca Raton.
- Wood, S.N., 2012. *gamm4: Generalized additive mixed models using mgcv and lme4*. R package version 0.1-6. <http://CRAN.R-project.org/package=gamm4>.

Electronic appendix: Location of study site and extent of the 1997 Olary Creek flooding.

Fig. 1. Average rainfall (mm) (☉), Minimum (■) and maximum (▲) temperature (°C) recorded at Scotia Station (Site Number 047105 Lat. 33° 12' 57" S; Long. 141° 10' 00" E, Elevation 50m). Scotia weather station is approximately 15 km south of our study site.

Fig. 2. Principal Response Curve analyses describing the change over time in plots subjected to fire, or flood or both, in contrast to those unaffected (horizontal control line). 3(a) Fenced plots; 3(b) unfenced plots (subjected to grazing by vertebrate species).

Fig. 3. Principal Response Curve analyses describing the change over time in plots subjected flood in contrast to those unaffected (horizontal control line). 3a) Fenced plots; 3b) unfenced plots. The 12 species with the strongest response (Resp.1) to the “treatments” are indicated.

Fig. 4. Change in species lifeform frequency over time in plots subjected to flood/no-flood and unfenced/fenced (protected from grazing by vertebrate species). Whiskers indicate SE.

Fig. 5. Model predictions (lines) and raw data (circles) showing the temporal response of the geometric mean diversity index to grazer exclusion. Dotted lines represent 95% confidence limits.

Table 1. Statistical outputs associated with the analysis of species diversity. Parametric estimates represent contrasts between fenced and unfenced plots, while outputs for the smoothed term, year, indicate variation from a flat temporal trend.