FEATURE PAPER

# Could biodiversity loss have increased Australia's bushfire threat?

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## Abstract

Ecosystem engineers directly or indirectly affect the availability of resources through changing the physical state of biotic and/or abiotic materials. Fossorial ecosystem engineers have been hypothesized as affecting fire behaviour through altering litter accumulation and breakdown, however, little evidence of this has been shown to date. Fire is one of the major ecological processes affecting biodiversity globally. Australia has seen the extinction of 29 of 315 terrestrial mammal species in the last 200 years and several of these species were ecosystem engineers whose fossorial actions may increase the rate of leaf litter breakdown. Thus, their extinction may have altered the rate of litter accumulation and therefore fire ignition potential and rate of spread. We tested whether a reduction in leaf litter was associated with sites where mammalian ecosystem engineers had been reintroduced using a pair-wise, cross-fence comparison at sites spanning the Australian continent. At Scotia (New South Wales), Karakamia (Western Australia) and Yookamurra (South Australia) sanctuaries, leaf litter mass (−24%) and percentage cover of leaf litter (−3%) were significantly lower where reintroduced ecosystem engineers occurred compared to where they were absent, and fire behaviour modelling illustrated this has substantial impacts on flame height and rate of spread. This result has major implications for fire behaviour and management globally wherever ecosystem engineers are now absent as the reduced leaf litter volumes where they occur will lead to decreased flame height and rate of fire spread. This illustrates the need to restore the full suite of biodiversity globally.

## Introduction

Ecosystem engineers directly or indirectly affect the availability of resources through changing the physical state of biotic or abiotic materials and, as such, they modify, maintain or create habitats either autogenically or allogenically (Jones, Lawton & Shachak, 1994). Beavers *Castor* spp. do this through their role in dam building, which affects geomorphology and ecology, and ultimately protects rare species (Bartel, Haddad & Wright, 2010). White rhinoceros *Ceratotherium simum* create grazing lawns that alter fire size and heterogeneity (Waldram, Bond & Stock, 2008). Plain's viscacha *Lagostomus maximus* promote fire heterogeneity by gathering vegetation for nesting sites, which ultimately alters vegetation patterns (Hierro *et al.*, 2011). Fossorial ecosystem engineers influence bioturbation and alter water infiltration, capture organic matter and increase nutrient cycling (Fleming *et al.*, 2014; Eldridge *et al.*, 2016).

The services provided by ecosystem engineers are frequently specific to individual species (Machicote, Branch & Villarreal, 2004; James *et al.*, 2011), suggesting functional redundancy is rare. Consequently, the extinction of ecosystem engineers means that the ecological function they provide is unlikely to be replaced by surviving species. The plethora of studies on the functions performed by ecosystem engineers reflect their importance within ecosystems, however, to date we know of no study that has illustrated the role fossorial mammalian ecosystem engineers play in regulating fire, despite this being hypothesized previously (Jones, Lawton & Shachak, 1996). In this study, we illustrate the role that fossorial ecosystem engineers play in leaf litter breakdown and how that translates to fire behaviour.

Uncontrolled wildfires cause enormous damage. For example, the total cost of 23 major wildfires in Australia between 1967 and 1999 was >$AUD2.5 billion with an additional human cost of 223 deaths and 4185 injuries (Australian

Institute of Criminology, 2004). In the USA, the 1998 Florida wildfire produced economic impacts of at least US $600 million (Butry *et al.* 2001) and fire suppression in the USA now exceeds $US1 billion per annum (Calkin *et al.*, 2005). Despite improvements in communications and technology, massive wildfires are still a common event in Australia, and with climate change, increasingly so (Marris, 2016).

Wildfire is a major conservation and land management issue globally with 179 mammal, 262 bird, 146 reptile, 300 amphibian and 974 plant species threatened by fire and fire suppression (IUCN, 2015). Leaf litter is the major source of combustible material to allow fire to spread, especially in mallee eucalypt communities (Bradstock, 1990), and fossorial species have the potential to reduce litter fuel loads (Nugent, Leonard & Clarke, 2014). Australia has suffered the loss of 29 medium-sized, ground-dwelling mammal species (Short & Smith, 1994; Johnson, 2006; Woinarski, Burbidge & Harrison, 2012), while numerous others are now restricted to offshore islands and so are extinct on the mainland (Burbidge, Williams & Abbott, 1997; McKenzie *et al.*, 2007; Woinarski *et al.*, 2012). Hence, the loss of these species in Australia means there is a high likelihood of cascading impacts that extend to fire regimes.

Herbivory is well documented as affecting fire regimes by removing fuel on plants and fuel that can fall as leaf litter (Leonard, Kirkpatrick & Marsden-Smedley, 2010; Ingram, Doran & Nader, 2013). Bioperturbating species, such as bower birds and lyrebirds, alter litter volume and distribution, and thereby reduce fire likelihood (Mikami *et al.*, 2010; Carvalho *et al.*, 2011; Nugent *et al.*, 2014). Here, we aimed to determine whether the extinction of members of Australia's critical weight range mammal fauna (Burbidge & McKenzie, 1989) has led to an increased accumulation of fuel that would potentially affect the rate of fire spread. This is timely given the directives of Australian state governments and Royal Commissions (Government of Victoria, 2011) regarding the area of control burns necessary to reduce the risk of life and property-threatening bushfires, despite the findings that this would only reduce bushfire risk by half (Price & Bradstock, 2011). It was originally proposed that 5% of all Crown Estate in Victoria would be burnt annually on a 20-year rotation (Recommendation 56 of the 2009 Bushfires Royal Commission; Government of Victoria, 2011), which is well below levels that would allow 'old growth' vegetation to form and provide habitat for old growth-dependent fauna (Clarke, 2008; Clarke *et al.*, 2010; Kelly *et al.*, 2011; Taylor *et al.*, 2012) and would negatively impact biodiversity (Giljohann *et al.*, 2015).

## Materials and methods

A pair-wise, fence-line comparison was replicated at three of the Australian Wildlife Conservancy's (AWC) faunal restoration sites spanning the Australian continent: Karakamia (284 ha in Western Australia's jarrah forest), Scotia (64 654 ha in far-western New South Wales) and Yookamurra (5108 ha in South Australia's Murrayland region;

Fig. 1). Karakamia receives 883 mm, Scotia 246 mm and Yookamurra 275 mm of rain per year (AWC, unpublished data). Scotia and Yookamurra are dominated by mallee eucalypt communities on linear dunes at Scotia and on thin soils overlaying calcrete at Yookamurra, while Karakamia supports jarrah forest. All sites have large fenced areas that exclude introduced predators (red foxes *Vulpes vulpes* and cats *Felis catus*) and competitors (European rabbits *Oryctolagus cuniculus* and livestock) and from where such species have been eradicated. Karakamia was fully fenced in 1994, Scotia in 2002 and 2006 (two separate 4000 ha areas), and Yookamurra in 2007. There have been no domestic herbivores on the properties since acquisition by AWC and large grazing macropod numbers are controlled within the fenced areas.

The vegetation at Scotia is generally in better condition than surrounding national parks due to a shorter pastoral history (Westbrooke, Miller & Kerr, 1998; Westbrooke, 2012). Karakamia and Scotia are situated within a matrix of largely intact vegetation, so human impacts on fire regimes are considered minimal (Archibald *et al.*, 2010), in contrast to Yookamurra, which sits partially within an agricultural landscape. In semi-arid areas, rainfall and soil moisture are limiting and limit litter decomposition rates, and the digging pits created by fossorial species are sources of higher humidity that promote litter breakdown, water infiltration and seed germination (Travers & Eldridge, 2012*a,b*).

Six previously extinct species (bilby *Macrotis lagotis*, boodie *Bettongia penicillata*, bridled nailtail wallaby *Onychogalea fraenata*, greater stick-nest rat *Leporillus conditor*, numbat *Myrmecobius fasciatus* and woylie *B. penicillata*) have been reintroduced to Scotia (Finlayson, 2010; Hayward, Herman & Mulder, 2010*a*; Hayward *et al.*, 2010*b*), four to Karakamia (woylie, southern brown bandicoot *Isoodon obesulus*, tammar wallaby *Macropus eugenii* and western ringtail possum *Pseudocheirus occidentalis*) and four of these have also been reintroduced to Yookamurra (bilby, boodie, numbat and woylie). Most of these species are considered as ecosystem engineers and their turnover of soil and litter could be expected to increase the rate of leaf litter breakdown (Garkaklis, Bradley & Wooller, 2004; James & Eldridge, 2007; James, Eldridge & Hill, 2009; James *et al.*, 2011). There is no difference in the arboreal folivore communities inside and outside the fenced areas as the fences are permeable to them, so any differences in litter volumes are unlikely to be driven by browsing effects.

Paired samples were taken from 1 m to the north of eucalypt trees growing 30 m inside and 30 m outside the fences at each of 21 locations at Scotia and 20 locations at Yookamurra and Karakamia spaced 1 km apart. These paired sites had similar vegetation, topography, fire ages and the trees selected all exceeded 0.2 m diameter at breast height. Areas beneath canopies are the major sites of litter accumulation in the mallee (Eldridge *et al.*, 2012). Each sample consisted of leaf litter collected in a 22 × 22-cm quadrat. This material was then sieved through 1 mm sieves and air dried for a month. At Scotia, we also compared the number of animal digging pits and logs inside and outside
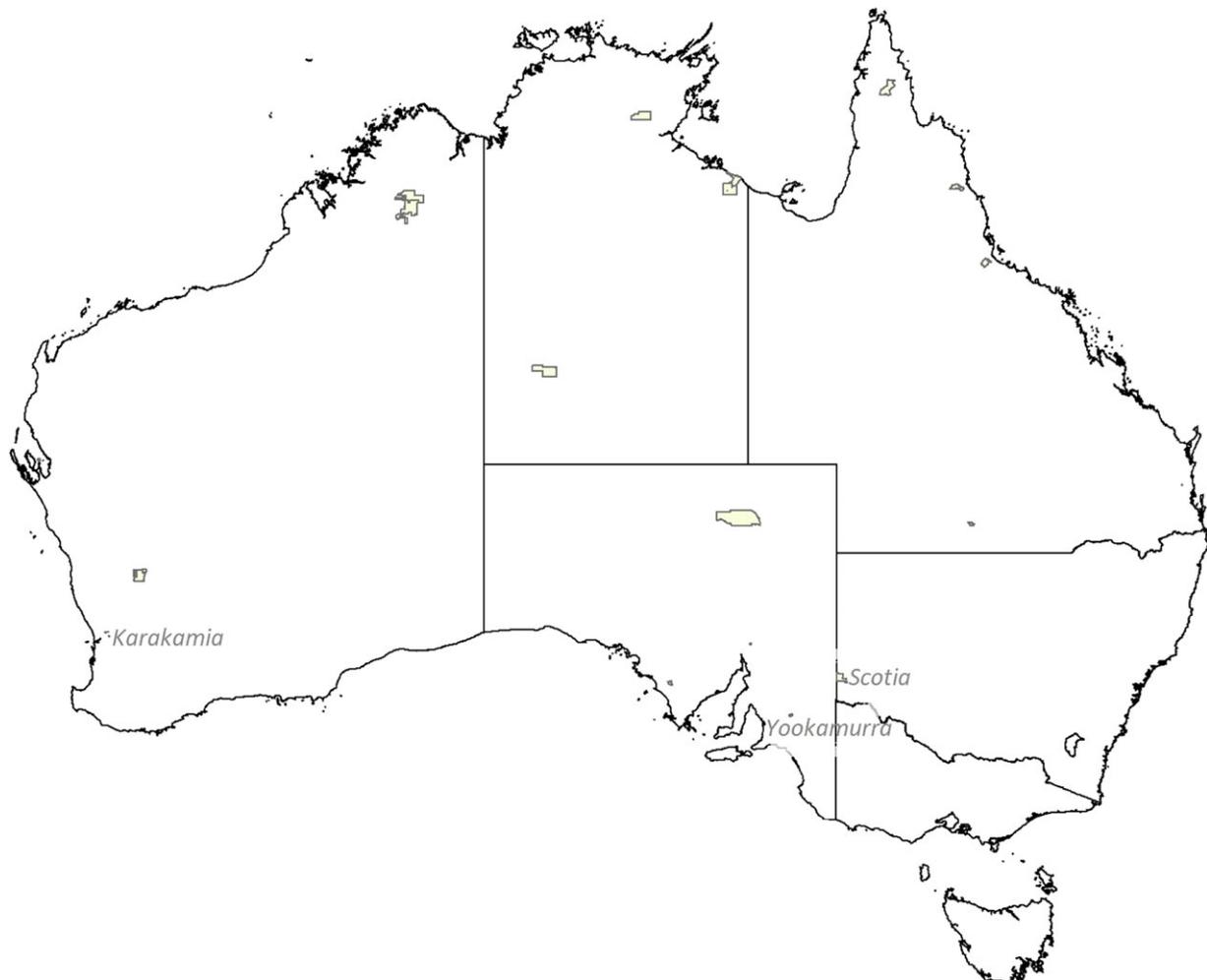
**Figure 1** Location map of the Australian Wildlife Conservancy's sanctuaries showing Karakamia, Scotia and Yookamurra.

the fences by counting them 1 m either side of a 50-m long transect, while percentage cover of cryptogamic crust cover, bare ground cover and vegetation cover were estimated visually by two observers.

Paired differences in leaf litter between fenced and unfenced plots were analysed using a linear mixed effect model in the *lme4* package (Bates *et al.*, 2013) in R (R Core Development Team, 2008) with site as a random effect. As absolute leaf litter levels varied strongly by site, relative change in levels in the unfenced plots was analysed. Ninety-five per cent (95%) confidence intervals for the relative differences were estimated using profile likelihood. Linear regression models were used to determine whether there was a difference in ground cover inside and outside the fences at Scotia. We also ran paired *t* tests on individual site data.

Finally, to assess how changes in leaf litter caused by reintroduced mammals might affect fire behaviour, we used mean fuel-load inputs from Scotia with conditions based on those experienced during a wildfire in September 2012 to run the McArthur Mk5 Forest Fire Behaviour model (Noble,

Gill & Bary, 1980). This model is widely used by fire services worldwide to predict the probability of fire starting, its rate of spread, intensity and suppression difficulty according to data on temperature, humidity, wind and drought conditions. On the day of the fire, maximum temperatures reached 37.5°C, relative humidity was 28% and winds reached 57 km $h^{-1}$ (data from Bureau of Meteorology online). We ran the models with drought conditions 5 and with a 0 ground slope following Nugent *et al.* (2014) and present data on both flame height as a measure of fire intensity and severity (Byram, 1959; Alexander & Cruz, 2012), and rate of spread. Data are presented as means $\pm 1$ SE.

## Results

Overall, the linear mixed effect model estimated a statistically significant 24% decrease (95% CI 6–43) in leaf litter mass in the fenced plots compared to the unfenced plots across sites. Scotia had significantly more leaf litter than Yookamurra and Karakamia (Fig. 2). The mass of leaf litter
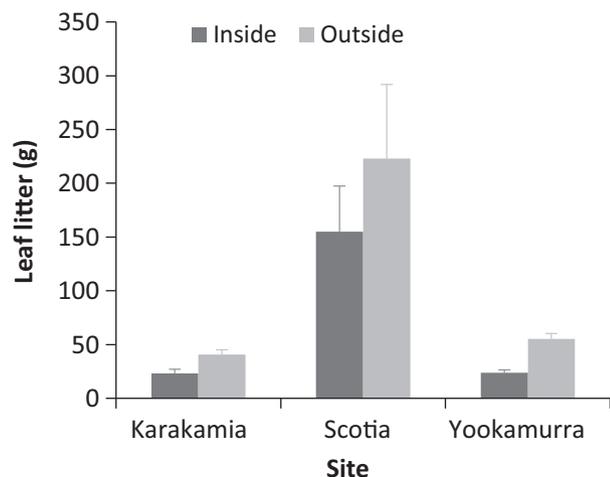
**Figure 2** Mean ($\pm 2$ SE) mass of leaf litter inside and outside fences at the Australian Wildlife Conservancy's Karakamia, Scotia and Yookamurra sanctuaries.

found inside the fences was significantly less at Karakamia ($23 \pm 2$ g cf $41 \pm 2$ g; paired $t_{19} = -6.586$, $P < 0.001$), Scotia ($155 \pm 21$ g cf $223 \pm 35$ g; paired $t_{20} = -2.158$, $P = 0.043$) and Yookamurra ($24 \pm 1$ g cf $55 \pm 3$ g; paired $t_{19} = -2.158$, $P = 0.046$; Fig. 2).

The linear model showed there was no significant difference in percentage ground cover inside and outside fences at Scotia, however, there were significant differences in ground cover types, as well as an interaction between fencing and cover type (Table 1). There was significantly less leaf litter cover inside Scotia's fenced areas compared to outside (Wald $\chi^2 = 13.495$, d.f. = 1, $P < 0.001$), but significantly more logs (Wald $\chi^2 = 37.432$, d.f. = 1, $P < 0.001$) and pits (Wald $\chi^2 = 29.272$, d.f. = 1, $P < 0.001$) inside fenced areas (Fig. 3). Leaf litter covers only 3% less area inside fences, but is 37% less in volume (dry weight) compared to sites outside the fences.

The McArthur fire behaviour model predicted flame heights during the September 2011 fire at Scotia to reach 1.41 m outside the fences compared to 0.37 m inside the fences. This model also predicted the fire to spread faster outside the fences (0.18 km h$^{-1}$) compared to 0.12 km h$^{-1}$ inside the fences. This equates to a 74% reduction in flame height and a 33% reduction in the rate of fire spread.

**Table 1** Generalized linear model results of the percentage ground cover at Scotia

| Source | Wald $\chi^2$ | d.f. | P |
|---|---|---|---|
| Intercept | 745.975 | 1 | <0.001 |
| Fenced/unfenced | 0.001 | 1 | 0.974 |
| Ground cover type | 326.629 | 5 | <0.001 |
| Interaction | 344.594 | 11 | <0.001 |

Wald post hoc tests revealed no effect of fencing on the area covered by any of the ground cover types at Scotia (bare earth, cryptogamic crust, leaf litter, logs, animal digging pits or vegetation).

## Discussion

This study highlights the benefits of reintroducing ecosystem engineers for the services they offer to fire management that have been lost from the majority of Australia's environment. These species probably play similar roles globally given the widespread distribution of fossorial species and the ubiquitous role that turning litter plays in speeding its breakdown. Such reintroductions may reduce the need for fire suppression and control in numerous fire-prone environments, which are costly and dangerous practices. The fossorial nature of the reintroduced marsupials has increased the rate of leaf litter breakdown compared to introduced fossorial species as native species dig deeper and wider pits than introduced rabbits Oryctolagus cuniculus due to the larger amount of litter and soil they turn over (Pollock, 2006; James & Eldridge, 2007; Eldridge et al., 2012). This in turn increases the return of nutrients into the soil (Elliot, Hunt & Walker, 1988; Eldridge et al., 2012). However, the reduction in available leaf litter also reduces fire spread as leaf litter is the biggest factor driving this (Bradstock, 1990). With reduced leaf litter, the risk of fire ignition is also reduced. Ultimately, a reduction in fire frequency is likely to slow the rate of carbon released into the atmosphere compared to current rates, because of the more rapid and complete release of carbon during fire than in the slow carbon pool driven by litter breakdown (Bond-Lamberty et al., 2007).

This is a global issue given reviews show that 447 mammalian genera spanning the globe have fossorial species that may significantly disturb the soil and leaf litter (Kinlaw, 1999) and many of these are likely to be threatened or locally extinct. Some taxa obviously turn over litter to increase decomposition rates. For example, Philippine porcupines Hystrix pumila are listed as vulnerable (IUCN, 2015) and, as fossorial rodents, are likely to affect litter decomposition (Bragg, Donaldson & Ryan, 2005). The rooting of suids clearly increases the rate of decomposition (Sandom, Hughes & Macdonald, 2013) and several of these are threatened including the Palawan bearded pig Sus ahoenobarbus, bearded pig S. barbatus, Visayan warty pig S. cebifrons, Oliver's warty pig S. oliveri, Philippine warty pig S. philippensis and the Javan warty pig S. verrucosus (IUCN, 2015). Fire is a major environmental problem in the range states of many of the species discussed above (Page et al., 2002).

A wildfire at Scotia provided additional support for the hypothesized ecosystem services provided by fossorial reintroduced fauna on fire behaviour. The fire burnt out rapidly where reintroduced ecosystem engineers were present, but continued to burn for several hours where they were absent (for further details see Supporting Information Appendix S1). While the relationship between leaf litter and bushfire is complex and each of our study sites is likely to respond differently to fire, we believe this anecdote illustrates the impact of the altered leaf litter cover and volume on fire behaviour.

It is important to point out the limitations of this study. There are potential differences between the inside and outside of the fences beyond the presence of ecosystem engi-
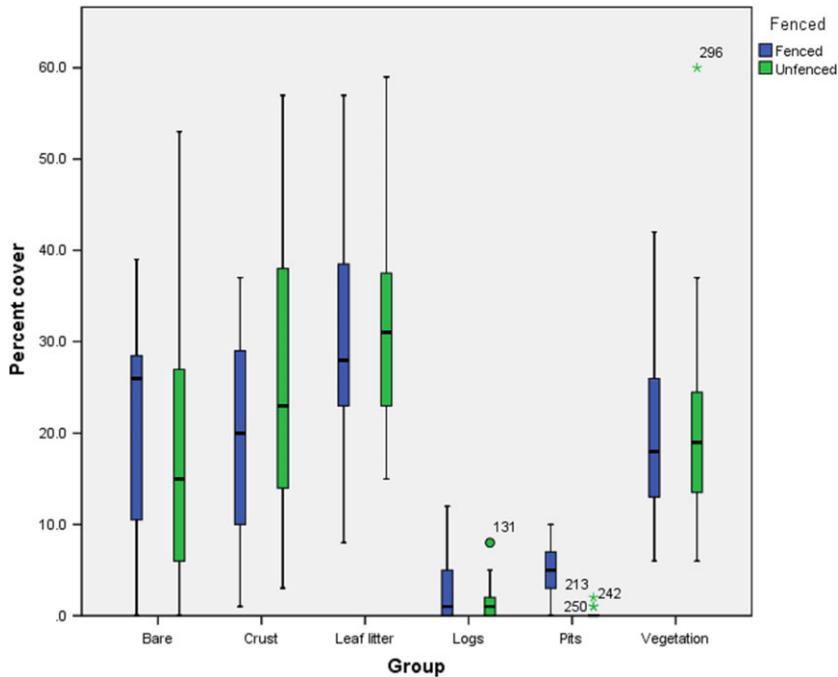
**Figure 3** Mean (±2 SE) percentage ground cover of bare earth, cryptogamic crust, leaf litter, logs, animal digging pits and vegetation inside and outside fences at the Australian Wildlife Conservancy's Scotia sanctuary. Significant differences based on Wald's chi-squared test are shown with asterisks (***$P < 0.001$).

neers including the presence of introduced herbivores (rabbits and goats *Capra hircus*), potential local rainfall variation and the reintroduced species within the fences may be at artificially high densities in the absence of dingoes *Canis lupus* and this may enhance the fuel differences. Future studies should investigate how the change in leaf litter cover and volumes that we found affects fire behaviour in the field. Nugent *et al.* (2014) did this using a chronosequence approach with superb lyrebirds *Menura novaehollandiae* and was able to model the impact on fire behaviour. Given the intensive fire management implemented by AWC at fenced reintroduction sites, there is scope to investigate this experimentally. Furthermore, the relationship between litter breakdown and the number of diggings is also worth investigating.

The broad-scale declines and localized extinctions of Australia's marsupial ecosystem engineers (Woinarski *et al.*, 2012) are likely to have impacted a vast array of ecological features, including fire regimes. Altered fire regimes are a threat to numerous species of biodiversity, and in New South Wales alone this includes 14 endangered ecological communities, 39 threatened plant species, 4 birds and 10 mammals (NSW Scientific Committee, 2012), highlighting that the loss of functionally unique species undermines entire ecosystems (O'Gorman *et al.*, 2011). Yet the most fire-prone forested environments of eastern mainland Australia are bereft of numerous species of critical weight range mammals and ecosystem engineers (e.g. Tasmanian bettongs *Bettongia gaimardi*, eastern barred bandicoots *Perameles gunni*, potoroos *Potorous* spp., etc.). Their value in reducing the impact and spread of fires may be further evidence of the need to restore them to the environment. Tasmania retains an intact herbivore fauna, but still experiences devastating fires sug-

gesting forest type may interact with ecosystem engineers to affect leaf litter breakdown or fire behaviour, and that, even in the presence of these fossorial species, extensive wildfires will still occur in Australia (albeit at a lesser frequency).

There have been questions about the efficacy of control burning in reducing bushfire risk (Bradstock, 2003; Pinol, Beven & Viegas, 2005; Brewer & Rogers, 2006). Fuel reduction burns theoretically reduce fuel loads and make fire suppression more feasible (Cheney, 1994), however post-fire leaf fall rapidly replenishes this source of fuel (Travers & Eldridge, 2012b). Also other factors, such as ambient weather and recent rainfall, affect fire behaviour (Price & Bradstock, 2011). This is the first study that identifies the potential fire suppressive effect of native mammalian fauna via the increased breakdown of leaf litter to reduce fuel loads. This is a fascinating issue as the decline of critical weight range fauna in Australia has been linked to altered fire regimes (Fitzsimons *et al.*, 2010; Woinarski *et al.*, 2010; Carwardine *et al.*, 2011), however, there may be a feedback loop relationship occurring with native fauna reducing fuel loads and thereby reducing their risk of increased predation following fire (McGregor *et al.*, 2014).

While this study focuses on the benefits of the restoration of Australian fossorial species, it has direct relevance to wildlife restoration and fire management globally. Throughout the world, mammals are declining and fossorial ecosystem engineers are no exception (Davidson, Detling & Brown, 2012). Thus, this study provides more evidence of the value of conserving these species and restoring them to sites where they have been extirpated, to avert the functional homogenization of the planet (Clavel, Julliard & Devictor, 2010). Furthermore, restoring ecosystem engineers is a practice that reduces fuel loads while maintaining the integrity of

the soil, and thereby yields cascading benefits to local ecosystems (Dombeck, Williams and Wood, 2004).

## References

Alexander, M.E. & Cruz, M.G. (2012). Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorch height. *Int. J. Wildl. Fire* **21**, 95–113.

Archibald, S., Nickless, A., Govender, N., Scholes, R.J. & Lehsten, V. (2010). Climate and the inter-annual variability of fire in southern Africa: a meta-analysis using long-term field data and satellite-derived burnt area data. *Global Ecol. Biogeogr.* **19**, 794–809.

Australian Institute of Criminology. (2004). *The cost of Bushfires*. Canberra: Australian Institute of Criminology.

Bartel, R.A., Haddad, N.M. & Wright, J.P. (2010). Ecosystem engineers maintain a rare species of butterfly and increase plant diversity. *Oikos* **119**, 883–890.

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2013). *lme4: linear mixed-effects models using Eigen and S4. R package version* 1. Vienna: R Core Development Team.

Bond-Lamberty, B., Peckham, S.D., Ahl, D.E. & Gower, S.T. (2007). Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature* **450**, 89–92.

Bradstock, R.A. (1990). Relationships between fire regimes, plant species and fuels in mallee communities. In *The Mallee lands: a conservation perspective*: 218–223. Noble, J.C., Joss, P.J. & Jones G.K. (Eds). Melbourne: CSIRO.

Bradstock, R.A. (2003). Protection of people and property: toward an integrated risk management model. In *Australia burning: fire ecology, policy and management issues*: 119–123. Cary, G.J., Lindenmayer, D.B. & Dovers S. (Eds). Melbourne: CSIRO Publishing.

Bragg, C.J., Donaldson, J.D. & Ryan, P.G. (2005). Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. *J. Arid Environ.* **61**, 261–275.

Brewer, S. & Rogers, C. (2006). Relationships between prescribed burning and wildfire occurrence and intensity in pine-hardwood forests in north Mississippi, USA. *Int. J. Wildl. Fire* **15**, 203–211.

Burbidge, A.A. & McKenzie, N.L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biol. Conserv.* **50**, 143–198.

Burbidge, A.A., Williams, M.R. & Abbott, I. (1997). Mammals of Australian islands: factors influencing species richness. *J. Biogeogr.* **24**, 703–715.

Butry, D.T., Mercer, E., Prestemon, J.P., Pye, J.M. & Holmes, T.P. (2001). What is the price of catastrophic wildfire? *J. Forest.* **99**, 9–17.

Byram, G.M. (1959). Combustion of forest fuels. In *Forest fire: control and use*: 61–84. Davis, K.P. (Ed.). New York: McGraw-Hill.

Calkin, D.E., Gebert, K.M., Jones, J.G. & Neilson, R.P. (2005). Forest Service large fire area burned and suppression expenditure trends, 1970–2002. *J. Forest.* **103**, 179–183.

Carvalho, K.S., Alencar, A., Balch, J. & Moutinho, P. (2011). Leafcutter ant nests inhibit low-intensity fire spread in the understory of transitional forests at the Amazon's forest-savanna boundary. *Psyche Entomol.* **2012**, 1–7.

Carwardine, J., O'Connor, T., Legge, S., Mackey, B.G., Possingham, H.P. & Martin, T.G. (2011). *Priority threat management to protect Kimberley wildlife*. Brisbane: CSIRO Ecosystem Sciences.

Cheney, P. (1994). The effectiveness of fuel reduction burning for fire management. In *Fire and biodiversity: the effects and effectiveness of fire management*: 9–16. Sosebee, R.E., Wester, D.B., Britton, C.M., McArthur, E.D. & Kitchen S.G. (Eds.). Canberra: Biodiversity Unit, Department of Environment, Sport and Territories.

Clarke, M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildl. Res.* **35**, 385–394.

Clarke, M.F., Avitabile, S.C., Brown, L., Callister, K.E., Haslem, A., Holland, G.J., Kelly, L.T., Kenny, S.A., Nimmo, D.G., Spence-Bailey, L.M., Taylor, R.S., Watson, S.J. & Bennett, A.F. (2010). Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Aust. J. Bot.* **58**, 363–372.

Clavel, J., Julliard, R. & Devictor, V. (2010). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* **9**, 222–228.

Davidson, A.D., Detling, J.K. & Brown, J.H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.* **10**, 477–486.

Dombeck, M.P., Williams, J.E. & Wood, C.A. (2004). Wildfire policy and public lands: integrating scientific understanding with social concerns across landscapes. *Conserv. Biol.* **18**, 883–889.

Eldridge, D.J., Travers, S., Val, J. and Kwok, A. (2012). *Ecosystem engineering studies at scotia sanctuary*. Kensington: University of New South Wales, Australian Wildlife Conservancy and the Office of Environment and Heritage.

Eldridge, D.J., Woodhouse, J., Curlevski, N., Hayward, M.W., Brown, M.E. & Neilan, B. (2016). Soil foraging animals alter the composition and co-occurrence of microbial communities in a desert shrubland. *ISME J.* **9**, 2671–2681.

Elliot, E.T., Hunt, H.W. & Walker, D.E. (1988). Detrital food-web interactions in north American grassland ecosystems. *Agric. Ecosyst. Environ.* **24**, 41–56.

Finlayson, G.R. (2010). *The reintroduction of medium-sized marsupials in western New South Wales*. PhD thesis, University of Sydney.

Fitzsimons, J., Legge, S., Traill, B.J. and Woinarski, J.C.Z. (2010). *Into oblivion? The disappearing native mammals of Northern Australia*. Melbourne: The Nature Conservancy.

Fleming, P.A., Anderson, H., Prendergast, A.S., Bretz, M.R., Valentine, L.E. & Hardy, G.E.S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Rev.* **44**, 94–108.

Garkaklis, M.J., Bradley, J.S. & Wooller, R.D. (2004). Digging and soil turnover by a mycophagous marsupial. *J. Arid Environ.* **56**, 569–578.

Giljohann, K., McCarthy, M., Kelly, L. & Regan, T. (2015). Choice of biodiversity index drives optimal fire management decisions. *Ecol. Appl.* **25**, 264–277.

Government of Victoria. (2011). *The 2009 Victorian Bushfires Royal Commission Final Report*. Melbourne: Government of Victoria.

Hayward, M.W., Herman, K. & Mulder, E. (2010a). Update of Australian Wildlife Conservancy re-introductions. *Reintrod. Spec. Group e-Newsletter* **1**, 11–12.

Hayward, M.W., Legge, S., Parsons, B.C., Page, M.J., Herman, K. and Mulder, E. (2010b). Woylie *Bettongia penicillata* (Potoroidae: Marsupialia) reintroduction as part of the Australian Wildlife Conservancy's Endangered Species Recovery Programme at Scotia Sanctuary, far western New South Wales, Australia. In *Global re-introduction perspectives: 2010: additional case studies from around the globe*: 202–207. Soorae, P.S. (Ed.). Abu Dhabi: IUCN Species Survival Commission's Reintroduction Specialist Group.

Hierro, J., Clark, K., Branch, L. & Villarreal, D. (2011). Native herbivore exerts contrasting effects on fire regime and vegetation structure. *Oecologia* **166**, 1121–1129.

Ingram, R.S., Doran, M.P. & Nader, G. (2013). Planned herbivory in the management of wildfire fuels. In *Herbivory*: 61–76. Barros, B. & Fernandes M. (Eds). Rijeka: InTech.

IUCN. (2015). *IUCN Red List of Threatened Species. Version 2014.3*. Available at: www.iucnredlist.org

James, A.I. & Eldridge, D.J. (2007). Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. *Biol. Conserv.* **138**, 351–359.

James, A.I., Eldridge, D.J. & Hill, B.M. (2009). Foraging animals create fertile patches in an Australian desert shrubland. *Ecography* **32**, 723–732.

James, A.I., Eldridge, D.J., Koen, T.B. & Moseby, K.E. (2011). Can the invasive European rabbit (*Oryctolagus cuniculus*) assume the soil engineering role of locally-extinct natives? *Biol. Invasions* **13**, 3027–3038.

Johnson, C.N. (2006). *Australia's mammal extinctions: a 50,000 year history*. Canberra: CSIRO Publishing.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* **69**, 373–386.

Jones, C.G., Lawton, J.H. and Shachak, M. (1996). Organisms as ecosystem engineers. In *Ecosystem management*: 30–147. Sampson, F.B. (Ed.). New York: Springer.

Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Haslem, A., Watson, S.J., Clarke, M.F. & Bennett, A.F. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Divers. Distrib.* **17**, 462–473.

Kinlaw, A. (1999). A review of burrowing by semi-fossorial vertebrates in arid environments. *J. Arid Environ.* **41**, 127–145.

Leonard, S., Kirkpatrick, J. & Marsden-Smedley, J. (2010). Variation in the effects of vertebrate grazing on fire potential between grassland structural types. *J. Appl. Ecol.* **47**, 876–883.

Machicote, M., Branch, L.C. & Villarreal, D. (2004). Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? *Oikos* **106**, 527–535.

Marris, E. (2016). Tasmanian bushfires threaten iconic ancient forests. *Nature* **530**, 137–138.

McGregor, H., Legge, S., Jones, M.E. & Johnson, C.J. (2014). Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS ONE* **9**, e109097.

McKenzie, N.L., Burbidge, A.A., Baynes, A., Brereton, R.N., Dickman, C.R., Gordon, G., Gibson, L.A., Menkhorst, P., Robinson, A.C., Williams, M. & Woinarski, J.C.Z. (2007). Analysis of factors implicated in the recent decline of Australia's mammal fauna. *J. Biogeogr.* **34**, 597–611.

Mikami, O.K., Katsuno, Y., Yamashita, D.M., Noske, R. & Eguchi, K. (2010). Bowers of the Great Bowerbird (*Chlamydera nuchalis*) remained unburned after fire: is this an adaptation to fire? *J. Ethol.* **28**, 15–20.

Noble, I., Gill, A. & Bary, G. (1980). McArthur's fire-danger meters expressed as equations. *Aust. J. Ecol.* **5**, 201–203.

NSW Scientific Committee. (2012). *Ecological consequences of high fire frequency – key threatening process listing*. Hurstville: Office of Environment and Heritage. Available at: http://www.environment.nsw.gov.au/threatenedspecies/EcologicalConsequencesFiresKTPListing.htm

Nugent, D.T., Leonard, S.W. & Clarke, M.F. (2014). Interactions between the superb lyrebird (*Menura novaehollandiae*) and fire in south-eastern Australia. *Wildl. Res.* **41**, 203–211.

O'Gorman, E.J., Yearsley, J.M., Crowe, T.P., Emmerson, M.C., Jacob, U. & Petchey, O.L. (2011). Loss of functionally unique species may gradually undermine ecosystems. *Proc. Roy. Soc. Lond. Ser. B.* **278**, 1886–1893.

Page, S.E., Siegert, F., Rieley, J.O., Boehm, H.-D.V., Jaya, A. & Limin, S. (2002). The amount of carbon released from

peat and forest fires in Indonesia during 1997. *Nature* **420**, 61–65.

Pinol, J., Beven, K. & Viegas, D. (2005). Modelling the effect of fire-exclusion and prescribed fire on wildfire size in Mediterranean ecosystems. *Ecol. Modell.* **183**, 397–409.

Pollock, M. (Ed.) (2006) *Fruit and vegetable gardening in Australia*. London: The Royal Horticultural Society.

Price, O.F. & Bradstock, R.A. (2011). Quantifying the influence of fuel age and weather on the annual extent of unplanned fires in the Sydney region of Australia. *Int. J. Wildl. Fire* **20**, 142–151.

R Core Development Team. (2008). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Sandom, C.J., Hughes, J. & Macdonald, D.W. (2013). Rooting for rewilding: quantifying wild boar's *Sus scrofa* rooting rate in the Scottish Highlands. *Restor. Ecol.* **21**, 329–335.

Short, J. & Smith, A.P. (1994). Mammal decline and recovery in Australia. *J. Mammal.* **75**, 288–297.

Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F. & Clarke, M.F. (2012). Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Divers. Distrib.* **18**, 519–529.

Travers, S.K. & Eldridge, D.J. (2012a). Above-average rainfall triggers an increase in fall rates of reproductive structures in an arid eucalypt woodland *Austral Ecol.* **38**, 820–830.

Travers, S.K. & Eldridge, D.J. (2012b). Landscape modulators and resource accumulation in a post-fire eucalypt woodland. *For. Ecol. Manage.* **285**, 11–19.

Waldram, M.S., Bond, W.J. & Stock, W.D. (2008). Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems* **11**, 101–112.

Westbrooke, M.E. (2012). The pastoral history, biological and cultural significance of the Scotia Country, far western New South Wales. *Proc. Linn. Soc. N. S. W.* **134**, A55–A68.

Westbrooke, M.E., Miller, J.D. & Kerr, M.K.C. (1998). The vegetation of the Scotia 1:100 000 map sheet, western New South Wales. *Cunninghamia* **5**, 665–684.

Woinarski, J.C.Z., Armstrong, M., Brennan, K.E.C., Fisher, A., Griffiths, A.D., Hill, B.M., Milne, D.J., Palmer, C.L., Ward, S., Watson, M., Winderlich, S. & Young, S.S. (2010). Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildl. Res.* **37**, 116–126.

Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2012). *The action plan for Australian mammals 2012*. Melbourne: CSIRO Publishing.

# Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Case study of the divergent response of a wild fire at Scotia in areas with and without reintroduced fossorial species.