

Temporal changes in soil function in a wooded dryland following simulated disturbance by a vertebrate engineer

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ABSTRACT

An inherent feature of arid and semiarid environments (drylands) is the importance of landscape heterogeneity in driving soil and ecological processes. Soil disturbance by organisms is an important, but often overlooked, driver of patchiness, but little is known about the temporal changes in soil and ecological processes following disturbance. We used artificial depressions, designed to mimic the foraging pits of the vertebrate marsupial, the Short-beaked echidna (*Tachyglossus aculeatus*), to examine temporal changes in soil labile carbon, decomposition, litter capture, and plant germination and survival, over an 18 month period. Foraging pits had a half-life of about 7 months, and trapped seven-times more litter than an equivalent area on the soil surface. Larger pits tended to trap more litter than smaller pits. Foraging pits trapped six-times more seed abundance and three-times more richness than the surface. Eighteen months after disturbance, litter decomposition was 30% greater in the pits, and labile carbon concentrations were 8% greater (622 mg kg^{-1}) than the original undisturbed soils (578 mg kg^{-1}). Taken together, we provide strong evidence that foraging by native animals is an important mechanism for driving spatial heterogeneity in dryland soils. Our results also suggest that simulating the activities of short-beaked echidnas may provide a mechanism for rehabilitating degraded soils.

1. Introduction

A distinctive feature of drylands (arid and semi-arid ecosystems) is the inherent resource patchiness, expressed at a range of spatial scales from individual plants to entire vegetation assemblages (Okin et al., 2009). Patches of enhanced resources, known variously as ‘fertility islands’ (*sensu* Garner and Steinberger, 1989) or fertile patches (Tongway et al., 1989) function as eco-hubs or bio-hotspots (Charley and West, 1975; Lejeune et al., 2002) within which nutrients, seeds, organic matter, and biological activity are elevated (Perroni-Ventura et al., 2010; Ochoa-Hueso et al., 2018), coupled (Tongway et al., 1989), and surrounded by a resource-poor matrix (Tongway and Ludwig, 1994).

Fertile islands also form as a result of intense foraging activity by soil-disturbing animal, ranging from invertebrates (Jouquet et al., 2006) to vertebrates (Whitford and Kay, 1999), whose soil movement alters soil physical and chemical properties while foraging for food or seeking shelter (Whitford and Kay, 1999). These soil disturbances are spatially non-random, and tend to be concentrated in preferred patches with more abundant resources (Eldridge et al., 2012), where shelter is more suitable, and often under the canopies of woody plants, where they

reinforce soil function. Although the impacts of animals on plants, soils and nutrient processes have been studied widely (e.g. Eldridge and James, 2009; Eldridge et al., 2015; Mallen-Cooper et al., 2019; Ross et al., 2019), the links between animal impacts and changes in soil and plant function are still relatively under appreciated. The reasons for this are twofold. First, there is a disconnect in scale between size, and therefore effects, of structures constructed by animals while foraging ($\text{m}^{-3}\text{-m}^{-2}$) and restoration processes, which are more closely aligned with landscape and sub-landscape scales ($\sim\text{m}^3\text{-m}^6$) (Jahantigh and Pessarakli, 2009). Few studies, therefore, have endeavored to upscale patch-level effects of soil-disturbing animals to landscape-level effects (though see Decker et al., 2019). Second, animal disturbances are highly spatially and temporally variable, so that studies based on naturally-constructed pits are compromised by spatial and temporal variation in disturbance size, shape, density, age and placement (e.g. Eldridge et al., 2016). For example, foraging pits constructed under the canopies of large trees will have different impacts on soil chemistry than those constructed in the open largely because the environment beneath trees is already nutrient enriched (see Eldridge and Rath 2002). Similarly, older foraging pits are likely to have a different suite of microorganisms

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compared to younger pits (Eldridge et al., 2015), constraining our capacity to make definitive conclusions about their impacts on ecosystem functions and therefore their role in soil restoration.

In order to explore temporal changes in plant and soil function following animal-induced soil disturbance, we used artificial depressions that mimic both the natural pits constructed by animals when they forage, and human-constructed pits, furrows and micro-catchments that are used extensively for soil reclamation (Gintzburger, 1987; Li et al., 2006; Abdelkadir and Schultz, 2005). We used as our model system the foraging pits constructed by Small-beaked echidnas (*Tachyglossus aculeatus*; Fig. 1a–c), because these engineers move substantial amounts of soil (Eldridge et al., 2015), and, unlike regionally-extinct vertebrate analogues, have not suffered from widespread predation by feral cats and foxes. Consequently, they still occur over most of the continent, and are good models with which to test soil restoration.

We have three aims. First, we expected that labile carbon (C), a measure of soil function, would decline markedly after disturbance due to the removal of the surface biocrust (aggregation of lichens and bryophytes), which is known to support high levels of C, and therefore the transfer of C-poor subsoil to the surface. Second, relatively little is known about the decomposition of litter trapped during the process of pit breakdown, and whether material covered by soil during this process will decompose at a faster rate than material laying of the pit surface soil during pit infilling. Specifically, we predicted greater decomposition of pit-resident litter covered by soil than uncovered litter because it would be more likely to come into contact with soil microbes (Torres et al., 2005). Finally, we expected that pits would support not only more seeds or greater diversity (e.g. James et al., 2010; James et al., 2011), but that pit-resident plants would survive longer than those growing on the adjacent undisturbed surface. Our study therefore aims to provide insights into the natural process of recovery of soils following soil disturbance by animals. This is important to encourage the promotion of strategies to protect soil-disturbing animals which might provide cheap and efficient methods to restore ecosystem functions (*sensu* Byers et al., 2006).

2. Methods

2.1. Study area

The study was conducted in a semi-arid woodland near Cobar in eastern Australia (−32.583°, 145.586°). The study site is about 530 km north-west of Sydney. The soils are predominantly Lixisols (IUSS Working Group WRB 2015) or Kandosols (Isbell, 1996); gradational

profiles that are characterised by loam to clay-loam surface textures up to 1 m deep overlying light-medium clay B horizons (Eldridge and Greene, 1994). The vegetation is typically open eucalypt woodland dominated by western red box (*Eucalyptus intertexta* R.T. Baker), white cypress pine (*Callitris glaucophylla* J. Thompson & L. Johnson) and wilga (*Geijera parviflora* Lindl.). The midstorey (shrub) layer comprises species plants of the genera *Dodonaea*, *Senna* and *Acacia*, and the understorey was dominated by perennial grasses such as speargrass (*Austrostipa scabra* (Lindl.) S.W.L. Jacobs & J. Everett), white-top grass (*Rytidosperma caespitosum* (Gaudich.) Connor & Edgar) and Jericho wiregrass (*Aristida jerichoensis* (Domin) Henrard). In most years the herbaceous vegetation occupies approximately 30–40% of the soil surface, with a similar proportion of the surface occupied by biocrusts (Eldridge and Greene, 1994). The average annual rainfall of 385 mm is highly temporally variable. Mean daily temperature in summer (January) varies from 11.1 °C to 46.7 °C (range 33.2 °C to 18.2 °C). Rainfall over the course of the study was generally well below the long-term average (Fig. 1d).

2.2. Field procedures

In June 2006 we established 25 stations (Blocks) about 50 m apart in an open *Eucalyptus intertexta* woodland. At a separation of 50 m, it was highly unlikely that any station would have influenced another, so we considered these stations to be statistically independent. At each block we constructed two artificial echidna foraging pits. Echidna pits are generally circular-shaped and surrounded by a small accumulation of rough or cloddy soil (Eldridge and Mensinga, 2007; Eldridge et al., 2011). We have been studying the attributes of echidna pits in the area for more than 5 years, enabling us to mimic, as closely as possible, the natural pits at the site. Artificial pits averaged 20 cm long by 22 cm wide by 8 cm deep, with an average volume of about 0.0037 m³ and surface aperture of 0.038 m².

We collected leaves of *Eucalyptus intertexta* from three live trees that had fallen over in a storm and placed approximately 5.0 (±0.1) g in each of 75 litter bags. Litter bags measured 10 cm by 10 cm and were constructed from nylon flyscreen mesh with a mesh size of 1 mm. Litter bags were placed in each of the 50 pits and secured to the soil with metal pins. An additional bag was secured to the surface within 10 cm of the pits. One of the pair of pits was randomly assigned to a treatment that covered the bag with soil. This was designed to simulate the trapping of litter beneath soil resulting from the initial animal disturbance or the infilling of pits by subsequent wind and water erosion. At each block, therefore, we had three litter bags, one remaining on the surface, one in a pit above the soil, and one in a pit covered with soil. Each of the 25 blocks was allocated randomly to five litter bag retrieval periods of 5, 7, 10, 14 and 18 months after litter bag placement.

At each of the designated retrieval periods, we measured the depth and two perpendicular diameters of each pit through the centre. Depth was measured to the top of the mineral layer. For pits filled with litter, the litter was carefully removed prior to depth measurements then replaced. Pit size was determined by calculating the area of the pit opening and pit volume calculated assuming half of a prolate sphere. After making pit measurements we carefully removed the bags from the surface and excavated the buried bag and placed them in plastic bags for removal to the laboratory.

2.3. Decomposition of *Eucalyptus intertexta* litter

Sand and inorganic material were carefully removed with a fine brush, the litter carefully washed and placed in an oven and dried at 110 °C for 24 h before being weighed. Data for dry matter remaining in the litter bags at each period were fitted to a negative exponential model (Olson, 1963) $x_t/x_0 = e^{-kt}$, where x_0 is the initial litter mass and x_t is the mass at time t , and k is the annual decay constant expressed in year^{−1} (Yahdjian and Sala, 2008). Separate regressions were performed for ln

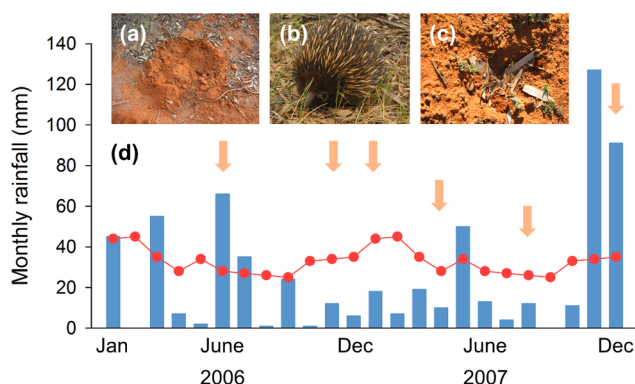


Fig. 1. (a) Recently constructed foraging pit at the commencement of the study, (b) photograph of the Short-beaked echidna (*Tachyglossus aculeatus*), (c) foraging pit at the end of the study (18-month old) showing accretion of soil and organic material, and (d) monthly rainfall (histograms) for the study site. The continuous line shows the mean monthly rainfall for the period 1981 to 2000 and the arrows represent dates when decomposition and labile carbon were assessed.

(x_t/x_0) for each of the three treatments to provide independent estimates of k ($n = 25$).

2.4. Litter and seed capture in the pits

At each of the five litter/seed sampling periods (November 2006, January, April, August and December 2007) we collected all litter accumulating in all pits and within a similar-sized area of the surface at each of the 25 blocks. The large spatial variability in litter accumulation across the study site meant that not all sampling sites contained litter at all times. We determined the total mass of litter after drying at 60 °C for 24 h and separated counted and identified to species all seeds found in the litter. Any soil removed during the litter removal process was carefully returned to the pits.

2.5. Plants germinating in the pits

We recorded all plants that had germinated within pits at 20 of the 25 blocks at three time periods 12 (July 2007), 13 (August 2007) and 16 (October 2007) months after pit construction. Pits at five of the blocks were destroyed by echidnas between the first and last sampling date, so were omitted from the analyses. These observations coincided with a large rainfall event in early July that stimulated a germination event. We did not discriminate between pits with or without soil. For each pit we counted all germinants, by species, within a circular 11 cm diameter quadrat and repeated this at a control location 11 cm away from the pit in a predetermined direction. Thus, at each block we had two pits, each with two adjacent control surfaces, resulting in 40 foraging pits and 40 control sites at each of the three sampling time periods.

2.6. Soil labile carbon

At each of the five sampling periods, and the at initial pit construction, we collected about 20 g of soil from the pits and the top 5 cm of the soil surface to compare temporal changes in labile C from pit construction to breakdown. Labile C was used as our measure of soil function because it represents the form of carbon that is most biologically active and closely related to biologically-mediated processes such as respiration, change in microbial biomass and soil aggregation than other measures of organic C (Weil et al., 2003). Further, the quality and concentration of labile C has been shown to influence decomposition rates (Adair et al., 2017). Labile C was determined using a simplified laboratory method whereby slightly alkaline, dilute KMnO_4 reacts with the readily oxidizable (active) C, converting Mn(VII) to Mn(II), and lowering the absorbance of 550 nm wavelength (Weil et al., 2003).

2.7. Statistical analyses

We used mixed-models General Linear Models (GLM) ANOVA to examine the effects of microsite (pit, pit with soil, surface), 5, 7 and 10 months after pit construction, on the daily rate of litter capture (using $\log_{10}(x + 1)$ – transformed data), seed abundance (no. of seeds), and seed richness (no. of species). We used a blocking term to account for the arrangement of microsites into blocks ($n = 25$). These three dates were selected because litter and seeds could readily be collected up until 10 months without destroying the integrity of the pits. For litter capture, we used the distance to the nearest large *Eucalyptus intertexta*, as a covariate to examine potential effects of proximity to litter source. The GLM structure had two strata. The first stratum considered Date ($n = 3$) and the fact that they are blocked, and the second stratum Microsite ($n = 3$) and its interaction with Date. Because litter and seed were removed at each sampling date, data for each time period were independent, and therefore a repeated measures GLM was unnecessary. Labile C data were analysed with a similar GLM model but over all time periods ($n = 6$).

The total mass of litter accumulating in the pits since the previous visit and the daily rate of litter accumulation were regressed separately

against pit aperture and volume using a range of linear and non-linear models (Payne 2009). The data for both pit types and all three recording periods were combined for the final model ($n = 33$ pits).

For analysis of germination within the pits over time we used a GLM structure with three strata; a Blocks stratum, a Blocks*Microsite stratum, and third stratum that accounted for sampling date and its interactions with Blocks and Microsite. To account for possible autocorrelation between successive sampling dates, the degrees of freedom for the Time and Time \times Microsite interaction were adjusted using the Greenhouse-Geisser epsilon measure within the Genstat package (Payne, 2009). A Greenhouse-Geisser epsilon value of 0.873 indicated that there was little correlation among dates. For all analyses, data were checked for normality and homogeneity of variance (Levene's test, Genstat) prior to GLM.

We used Permutational Multivariate Analysis of Variance (PERMANOVA–Anderson, 2017) to examine possible differences in the spectrum of seeds found in litter, and plants emerging, in the three microsites for the three time periods (and their interactions). The degree of association of individual plant species with the three microsites (averaged over the three time periods) was measured with Indicator-Species Analysis (Dufrene and Legendre, 1997) using the PC-ORD (McCune and Mefford, 1999) statistical package. Indicator values combine information on relative abundance and frequency of species. The indicator value is maximal (IV = 100) when all individuals of a given species are restricted to a particular microsite, and all samples from the particular microsite contain an occurrence of that species. Species data were randomized among the microsites and ripping status, and a Monte Carlo randomization procedure performed with 1000 iterations in order to determine the statistical significance of the indicator values.

3. Results

Artificial foraging pits filled rapidly, with a volume half-life of 7 months (Fig. 2). The rate of pit infilling, measured as the change in pit depth, was best described by an exponential decay function of the form (Fig. 2). *Eucalyptus intertexta* leaves decomposed at a relatively constant rate of about 3.0 to 3.8% per month, but decomposition was most marked during the final 6 months of the study (4.1 to 5.0% per month; Fig. 3a). K -values for decomposition were more similar for the surface (0.112) and pit-covered (0.114) microsites than the open pit (0.135). By the end of the study, there was significantly greater decomposition of leaves in both the pits where leaves were covered (68.4%) or uncovered (65.0%) than on the surface (51.4%) ($F_{2,40} = 5.02$, $P = 0.011$; Fig. 3a). Some litter bags were invaded by termites, which penetrated the fiberglass mesh. Despite this, there were no significant differences in decomposition between termite-invaded and termite-free bags (t -test; df

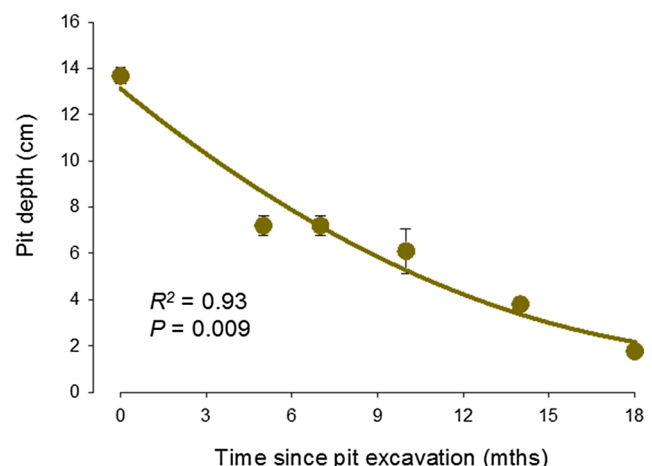


Fig. 2. Mean (\pm SE) depth of foraging pits over 18 months.

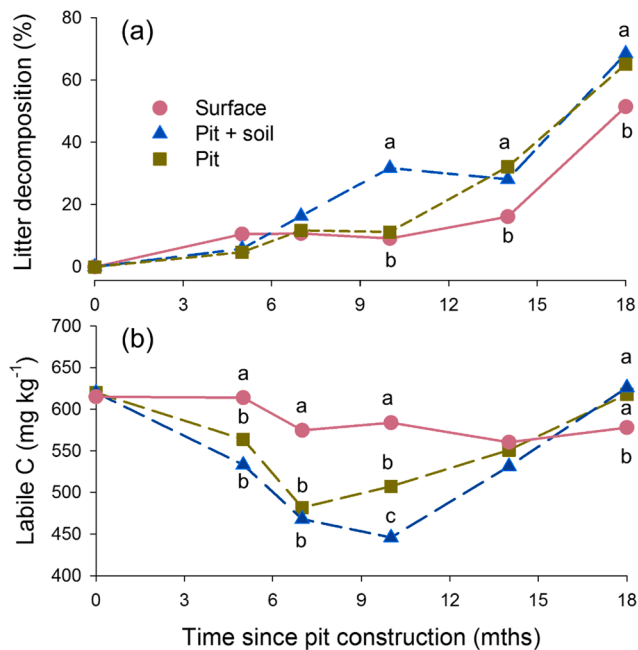


Fig. 3. (a) Mean litter decomposition (%) and (b) concentrations of labile soil C (mg kg^{-1}) up to 18 months after pit construction for the three microsites. Different letters within a given date indicate differences in litter decomposition or labile C among the three microsites.

= 5, $P = 0.97$). Soil labile carbon changed markedly over time, declining immediately following pit construction, and was less than the surface for the next 14 months (Fig. 3b). By 18 months after disturbance, labile carbon was significantly greater in the two pit treatments than the surface ($F_{2,40} = 5.31$, $P = 0.009$; Fig. 3b).

3.1. Litter capture within the pits

Pits trapped about seven-times more litter (12.7 ± 3.12 g; mean \pm SE) than a similar-sized area on the surface (1.91 ± 1.13 g; $F_{2,42} = 7.41$, $P = 0.002$). This was reflected in the daily litter capture, with 0.14 g pit $^{-1}$ day $^{-1}$ compared with 0.02 g day $^{-1}$ for a similar area of non-pit ($F_{2,42} = 7.41$, $P = 0.002$ on $\log_{10}(x + 1)$ -transformed data). Using distance from large eucalypts as a covariate in the ANOVA models did not improve our ability to predict rates of litter capture. Pits of larger volume with larger apertures trapped more litter (pit volume: $F_{1,31} = 6.7$, $P = 0.013$, $R^2 = 0.16$; pit aperture: $F_{1,31} = 13.1$, $P = 0.001$, $R^2 = 0.28$).

3.2. Abundance and diversity of pit-captured seed

We collected a total of 5,026 seeds from litter at the three periods over all treatments. Overall, seeds were six-times more abundant in the two pit treatments (56.4 to 67.5 seeds) than the surface (10.0 seeds) treatment ($F_{2,42} = 6.20$, $P = 0.004$), and this was consistent among the three time periods (Microsite \times Time interaction: $P = 0.95$). Seed richness mirrored that of abundance, with three-times more species in the two pit treatments (3.3 to 3.9 species) than the surface (1.0 species; $F_{2,42} = 22.1$, $P < 0.001$). Multi-variate analyses of the seed species matrix showed that although the two pit treatments differed slightly from the surface microsite in their complement of species ($P = 0.04$), the main species accounting for this difference, *Maireana sclerolenioides* was not strongly indicative of pit soils (Indicator Value (IV) = 17.0, $P = 0.03$).

In general, pits with more litter had significantly greater seed richness ($F_{1,48} = 7.16$, $P = 0.01$, $R^2 = 0.14$; Fig. 4a) and more seeds ($F_{1,48} = 16.9$, $P < 0.001$, $R^2 = 0.25$; Fig. 4b). The predictive power of these relationships was unchanged when we included distance from the pits to patches of litter (e.g. mounds of coarse woody debris) in the analyses.

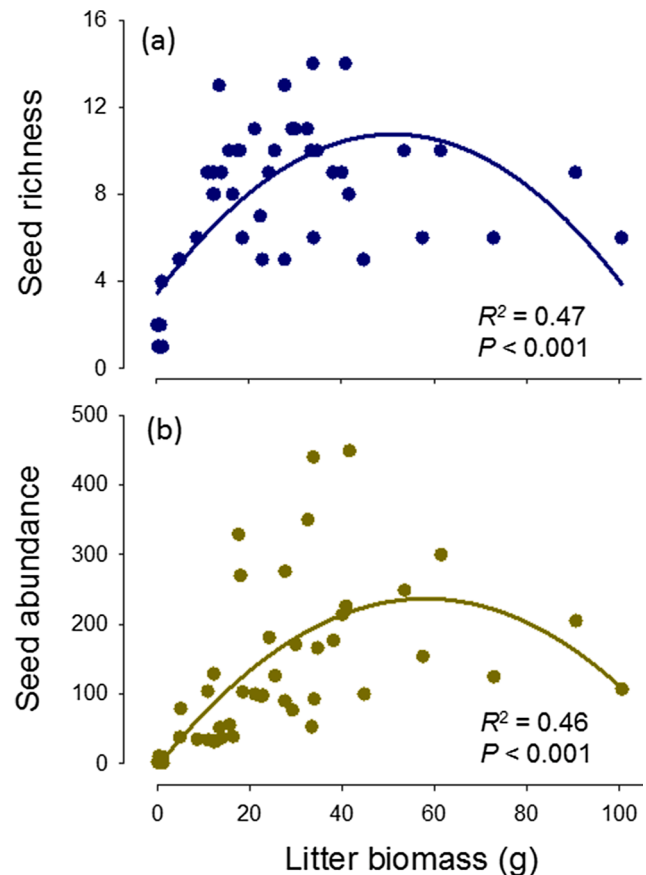


Fig. 4. Relationships between litter biomass (g) and (a) richness and (b) abundance of seeds trapped in litter across the three microsites.

3.3. Plants germinating in the pits

Significantly more plants germinated in both type of pits (mean = 18.6 to 19.4 plants per pit) than on the surface (6.5 plants per pit; $F_{2,38} = 11.81$, $P < 0.001$ on $\log_{10}(x + 0.1)$ -transformed data). Similarly, twice as many species germinated in both pit microsites (3.6 to 3.7 species per pit) than on the surface ($F_{2,38} = 8.62$, $P < 0.001$). Both richness and abundance of germinants in the pits declined over time ($P < 0.001$).

There were strong and significant differences in the complement of germinants between pit and surface microsites ($P = 0.002$) and significant differences among the three time periods ($P = 0.002$), but no significant Time by Treatment interactions ($P = 0.75$). Typical species indicative of pits were *Cuphonorhynchus humistratus* (IV = 64.2, $P = 0.005$), *Actinobole uliginosum* (IV = 59.8, $P = 0.001$), *Goodenia pusilliflora* (IV = 45.9, $P = 0.003$) and *Erodium crinitum* (IV = 37.1, $P = 0.006$). There were no significant indicators of surface microsites.

4. Discussion

We examined how simulated depressions or micro-catchments, designed specifically to mimic the foraging pits of short-beaked echidnas, capture resources, alter decomposition and soil C, and affect plant germination in a semi-arid woodland. We found that our model pits captured more seed and litter, had a greater abundance and richness of plant germinants, and functioned as significant sinks for organic matter over a period of 18 months. Importantly, our work indicates that these structures develop into resource-rich niches relatively rapidly, providing an important source of spatial heterogeneity that is critical for the functioning of drylands systems. Our work also suggests that the activity of soil-foraging animals may have an important role, not only in fostering spatially heterogeneous patches of soil, but by initiating the

rehabilitation of degraded dryland soils.

4.1. Rapid recovery of labile C in the pits

We found significantly lower concentrations of labile C in the pits, likely due to the removal of biocrusts, which occupy about 40% of the surface of these soils (Eldridge and Greene, 1994). Biocrusts support a diverse microbial community responsible for a high activity of enzymes such as cellobiosidase, β -glucosidase and invertase (Delgado-Baquerizo et al., 2015), which are involved in carbon cycling (Miralles et al., 2012). Removal of the biocrust during topsoil excavation likely alters soil biological activity by reducing the capacity of soils to catalyze sucrose and decompose cellulose and related polysaccharides (Delgado-Baquerizo et al., 2015). Recovery of labile C concentrations to pre-disturbance levels occurred after about 15 months, corresponding to the time when the pit was about 75% full, and a period of increased decomposition. *Eucalyptus* leaves decomposed 30% faster in the pits than on the surface, and the fact that decomposition was similar in termite-invaded and termite-free litter bags suggests that the main mechanism driving this decomposition is microbial (fungal).

Pits trapped more litter, consistent with global studies of a range of surface-disturbing animals (e.g., Whitford and Kay, 1999; James et al., 2010; Davies et al., 2019; Mallen-Cooper et al., 2019). Greater litter capture should equate with more labile C, so that increasing labile C should track changes in pit infilling by organic matter and soil. However, the initial rates of labile C production depend on litter quality (e.g. the lignin-to-nitrogen ratio), age and the degree to which a large litter mass is packed into a relatively small space (Cornwell et al., 2008). Apart from our decomposition study substrate, much of the litter falling into the pits was *Eucalyptus* leaves, which are generally low in N due to their tendency to resorb substantial N before abscission (Wendler et al., 1995). Old leaves are likely, therefore, to provide only a source of recalcitrant carbon, which is likely to accumulate as the labile C is rapidly respired by microorganisms. The low levels of labile C during the pit recovery process result from the high microbial N demand during the decomposition of N-poor *Eucalyptus intertexta* substrates (Cookson et al., 2006). Our study suggests that this period of low labile C availability lasts for about 15 months, by which time successional shifts in microbial communities (e.g. changes in fungal-to-bacterial ratio) are likely to occur. Increases in the fungal-to-bacterial ratio have been shown to accelerate mineralization in soils of low quality litter (Sardans et al., 2012), and this ratio may be more important than litter quality in determining soil carbon availability (Delgado-Baquerizo et al., 2015). Recovery of labile C with pit age could also have been due to increased root biomass, and therefore greater levels of root exudates, of plants establishing in the pits (Mergel et al., 1998). It is likely that low levels of labile C during the pit recovery process result from the high microbial N demand during the decomposition of N-poor *Eucalyptus* substrates (Cookson et al., 2006).

4.2. Pits as refugia for germinants

Artificial foraging pits contained six-times more seed and three-times greater seed richness than the equivalent area of surface soil. Furthermore, there was three-times greater seed germination in the pits, providing compelling evidence of the importance of foraging pits as sinks for seed (Dundas, 2018; James et al., 2010; Valentine et al., 2017). Although we collected a large number of seeds from the pits, only a small proportion were present in the germinant pool, and differences in germination probably relate to idiosyncratic differences in germination cues for different taxa, or the fact that large numbers of seeds could have been removed by ants or rodents prior to germination. Some of the original seed cache species in these woodlands are known to be important prey items of ants, and differences between pits and surface probably reflect differences in removal efficiency by ants. Surface seeds, in particular, are likely more susceptible to predation than those in the pits (e.g. Steinberger and Whitford, 1983; Gutterman and Herr, 1981;

Whitford, 2002; James et al., 2010). Indeed, seed removal experiments at our study site indicate that the small-bodied, dominant *Dolichorine* ants *Iridomyrmex* spp. are able to remove seed from the soil surface five-times faster, on average, than from artificial echidna pits (Radnan and Eldridge, 2017). Pits may therefore become caches of seed simply due to the high energy costs of removal by ants, the major secondary seed dispersers in arid Australia.

We found some differences in plant composition between pits and surface. While Indicator Species Analysis showed that four species (*Cuphonotus humistratus*, *Actinobole uliginosum*, *Goodenia pusilliflora* and *Erodium cicutarium*) were moderately indicative of pit microsites, no species were significant indicators of surface locations. The four pit species are found extensively across the landscape, in a range of habitats, suggesting that either pits are unlikely to provide novel habitat for pit-obligate species, or that 200 years of grazing by European livestock has removed those species that are tied strongly to disturbances created by native soil foraging animals, including the echidna. Plants present in the pits survived longer than those on the surface, likely due to higher soil moisture holding capacity (Eldridge and Mensinga, 2007), and potentially, moderation of environmental conditions and differential microbial community composition (Davies et al., 2019).

Most plant germination occurred in the pits rather than the mounds of accreting soil that typically surround echidna foraging pits (Eldridge et al., 2012). Studies of other soil disturbing animals have shown that these accretion mounds, such as those constructed by American badgers (*Taxidea taxus*; Eldridge and Whitford, 2009), have relatively high C:N ratios, and may favour native plants over exotics due to low levels of soil available N, which gives native plants a competitive advantage over nitrophilous exotic plants. Our data suggest therefore, that we might expect a different suite of species depending on the extent to which C-poor soils are transported from the subsoil to the surface, given their effects on soil C levels. In a restoration context, therefore, the depth of soil excavation would likely determine the nature of the suite of species germinating.

Current information on pit infilling suggest that pits would be almost indistinguishable from surface soil within 3 years (Eldridge, 2011), consistent with predictions based on the size of these structures (Whitford and Kay, 1999). Our studies from eastern Australia indicate a relatively low (<3%) landscape-level cover of echidna foraging pits, though their distribution is highly clustered around woody vegetation (Eldridge et al., 2012). In a restoration context, in order to simulate the highly clustered pattern of these foraging pits, the placement of artificial pits would need to be more selective. Regular construction of pits with mechanical methods that fail to emulate their unique placement likely accounts for some of the lack of restoration success during widespread reclamation programs (Tongway and Ludwig, 2010).

We used artificially constructed pits rather than those constructed naturally by echidnas to remove any potential biases associated with differential pit size, age, placement or orientation, which have been shown to influence the effects that pits have on litter and seed capture (e.g. Eldridge and James, 2009). Because our pits were artificial, we were unable to detect potential effects of microbes or fungi that might have been dispersed by echidnas during their foraging. Although not determined experimentally, echidnas will almost certainly disperse soil microbes on fleshy noses, as has been demonstrated with respect to dispersal of fungal spores by long-nosed bandicoots (*Perameles nasuta*; Vernes and Dunn, 2011). In studies of bilby (*Macrotis lagotis*) foraging pits, we found that younger pits were dominated by opportunistic fungi with aggressive colonizing strategies that were relatively tolerant of high temperatures (Houbraken and Samson, 2011; Eldridge et al., 2015). Older pits, however, tended to support more cyanobacterial species that originated from the thin biocrusts on the undisturbed surface (Eldridge et al., 2015). Thus, given the potential absence of echidna-dispersed spores and microbes in our pits, their effects on decomposition and labile carbon concentrations are likely to have been less than that in natural pits.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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