The resource coupling role of animal foraging pits in semi-arid woodlands

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ABSTRACT

Water is a strong driver of ecosystem function and diversity in resource-limited drylands. Structures that alter the redistribution of water have the potential to affect vegetation pattern and productivity and the maintenance of spatial heterogeneity. We examined the role of surface foraging pits and mounds constructed by the short-beaked echidna (*Tachyglossus aculeatus*) on runoff generation, sediment detention and seed capture. We speculated that pits dug into biologically crusted interspace soils would reduce overland flow and act as sinks for seed, while mounds of ejected soil would increase sediment availability. Runoff and sediment yield were examined under simulated rainfall with five levels of disturbance representing the pits and mounds of echidnas. Increasing the level of disturbance up to 47% cover of mounds and pits had no effect on time to ponding, steady-state runoff or the coefficient of runoff. However, time to initiation of runoff, sediment removal rates and sediment concentration in runoff water increased with increasing disturbance. Pit-to-pit and surface-to-pit movements of *Dodonaea viscosa* seed tended to increase, while pit-to-surface movements tended to remain unchanged with increasing disturbance. Surface-resident seed generally moved shorter distances with increasing disturbance. The results highlight the importance of mounds and pits of soil foraging animals for generating and trapping eroded sediment. Runoff and erosion processes may therefore provide a mechanism for coupling critical resources such as seed, water and sediment in resource-rich patches that will contribute to the development of small-scale heterogeneity in woodlands. Copyright © 2010 New South Wales, Australia.

KEY WORDS   echidna; resource coupling; runoff; soil erosion; foraging pits; cryptogamic crust; seed dispersal; hydrochory; *Tachyglossus*

Received 4 May 2010; Accepted 6 June 2010

INTRODUCTION

Studies in resource-limited environments worldwide indicate that essential resources such as water, organic matter, soil, seed and nutrients are concentrated within patches or sinks (islands of fertility, fertile patches *sensu* Garner and Steinberger, 1989) in a relatively unvegetated, resource-poor matrix (Ludwig *et al*., 2005). Zones of higher resource concentrations range from groves of woody vegetation (Wakelin-King, 1999; Tongway *et al*., 2003) to individual plant tussocks and hummocks whose physical structure provides a mechanism for sequestering and retaining resources (Bochet *et al*., 2006; Bolling and Walker, 2002). These resource-rich vegetated patches act as reserves of higher productivity and diversity within a relatively infertile matrix (Bolling and Walker, 2002).

Runoff, a consequence of water redistribution, is a fundamental ecological process in arid and semi-arid (dryland) systems. Redistribution of runoff is thought to be a significant driver of resource patchiness (Ludwig and Tongway, 1995; Seghieri and Galle, 1999; Shachak *et al*., 1999) and occurs when rainfall intensity exceeds the soil's infiltration capacity (Wilcox *et al*., 2003). This redistribution transfers water, sediment, seed and

organic matter among the vegetated patches, connecting patches that would otherwise be isolated (Belnap *et al*., 2005). Extensive, human-induced disturbances reduce the capacity of dryland ecosystems to sequester and retain resources so that systems become non-conserving (Wilcox *et al*., 2003; Ludwig *et al*., 2005). For example, extensive overgrazing in drylands reduces vegetation cover and therefore infiltration rates, increasing erosion rates and resulting in feedback processes on subsequent plant growth (Rietkerk and van der Koppel, 1997). While rainfall may produce sufficient subsoil moisture for plant production, the soil nutrient pool may be well below threshold concentrations, so that water and nutrients are 'decoupled', thus preventing an ecological response.

Notwithstanding the devastating effect of large-scale human-induced disturbances, small-scale disturbances may be important for ecosystem stability and productivity, particularly if they complement rather than compromise the relationships between resource accumulating and resource shedding areas. One such disturbance type, which may play important roles in resource distribution, results from the activities of ground-dwelling, semi-fossorial (digging) animals (Whitford and Kay, 1999). Soil disturbance by animals results in patches of soil that reduce the velocity of overland flow and capture transported organic matter. They therefore differ physically and chemically from the surrounding undisturbed soil. The foraging pits of the African Crested Porcupine

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(*Hystrix cristata*) in the Negev Desert, for example, are microsites of higher nutrient concentrations and enhanced plant germination and productivity (Boeken *et al.*, 1995). Similarly, foraging pits of the reintroduced Greater bilby (*Macrotis lagotis*) and Burrowing bettong (*Bettongia lesueur*) have been shown to be more resource-rich, with greater amounts of water and litter, higher concentrations of labile and total carbon, total and mineralizable nitrogen and more abundant vascular plants (James and Eldridge, 2007; James *et al.*, 2009).

Australian drylands have suffered significant mammal extinctions in the 200 years since European settlement, and many soil-disturbing fauna have been lost from the mainland or are extinct. One soil-disturbing mammal, the short-beaked echidna (*Tachyglossus aculeatus*), is still relatively common over large areas of the continent. Echidnas, known colloquially as spiny anteaters, excavate pits while foraging for epigeic invertebrates such as termites and ants, moving up to 2 t soil ha^{-1} in the form of small conical pits, scratchings and areas of extensive surface activity (Rismiller, 1999; Eldridge and Kwok, 2008). In the semi-arid woodlands, echidnas forage extensively in the plant interspaces (matrix), which are characterized by long, gentle slopes supporting biological soil crusts, perennial grasses and forbs (Eldridge, 1998). The crusts are strongly hydrophobic, and redirect water into the vegetated run-on zones (Eldridge, 1998). Field observations suggest that echidna foraging pits act as microcatchments for water, and the adjacent ejecta material, which is excavated from the pits and inverted on the soil surface, acts as a source of sediment for areas downslope.

Here, we speculate that foraging by echidnas provides a mechanism for the coupling of water, sediment, organic matter and seed by influencing runoff and erosion processes. Unconsolidated soil ejecta discarded from the pits would be expected to be mobilized by overland flow and deposited in the pits, along with runoff water- and surface-borne litter and seed. We tested this notion by simulating rainfall (and runoff) on artificially created echidna foraging pits and their associated mounds, and measured a range of soil hydrological properties along a gradient of increasing animal disturbance. We also measured the movement of seeds in runoff water to test the notion that pits would act as sinks for seed, irrespective of whether they originated from the pits or the interpit areas. We expected that increasing disturbance by echidnas would lead to increased soil erosion, but that pits would also act as retention basins, capturing smaller volumes of water and retarding the commencement of runoff.

METHODS

The study site

This study was conducted at Yathong Nature Reserve, 140 km southwest of Cobar in western New South Wales (145°35'E, 32°56'S), Australia. Although sheep grazing on native pasture is the principal land use in the region, the reserve has not been grazed by sheep since 1977 and supports a relatively undisturbed and extensive soil crust community (Eldridge and Greene, 1994). The reserve currently carries large populations of rabbits and kangaroos, is considered to be in relatively good rangeland condition and displays abundant evidence of echidna activity.

The study site occurs within the ridges and slopes unit of the Yackerboon Land System and is characterized by long low-ridge slopes to 2% slope and up to 1 km long. The soils have been described as Typic Haplargids (Eldridge and Koen, 1993), with surface textures ranging from loams to clay loams. Soil pH averages 6·5, electrical conductivity 0·32–0·36 dS m^{-1}, organic carbon 0·87% at 10 cm to 0·59% at 40 cm and surface soil aggregates are moderately stable (37% >2·0 mm; Eldridge and Koen, 1993). The mean maximum temperature for January is 33·1 °C and the mean minimum temperature is 18·2 °C. The mean January rainfall is 35·5 mm and the average annual rainfall is 383·8 mm (BOM, 2008). At the time of the study the mean daily maximum and minimum temperatures were 34·9 and 19·9 °C, respectively (BOM, 2008). In the week preceding this study, there was substantial rainfall (55 mm).

The reserve supports a vegetation community representative of that found over much of the red earth soils in the Cobar area. The vegetation is open to dense woodland dominated by red box (*Eucalyptus intertexta*), bimble box (*E. populnea* ssp. *bimbil*), white cypress pine (*Callitris glaucophylla*), wilga (*Geijera parviflora*), rosewood (*Alectryon oleifolius*) and mallees (*Eucalyptus* spp.). The understorey is dominated by perennial grasses such as speargrass (*Austrostipa scabra*), No. 9 wire grass (*Aristida jerichoensis*), kerosene grass (*Ar. contorta*) and white top grass (*Austrodanthonia caespitosa*) with an average ground cover of 45–55% (Eldridge and Koen, 1993). At the time of the study the ground-storey vegetation was dominated by paper daisies (*Rhodanthe* spp.), crimson foxtail (*Ptilotus atriplicifolius* var. *atriplicifolius*), common crowsfoot (*Erodium crinitum*), corrugated sida (*Sida corrugata*), copperburrs (*Sclerolaena* spp.) and a mixture of annual forbs.

Site selection

All soil hydrological measurements were made within five 100-m-long blocks aligned down the slope, parallel to each other and spaced about 300 m apart. Each block contained five 0·84 m × 0·84 m plots. Plots selected for rainfall simulation were selected on the basis that they were undisturbed, i.e. showed no obvious evidence of erosion, contained no perennial plants, had sparse cover of vascular plants and were on a similar slope (∼1%).

Pit construction

Artificial echidna foraging pits were constructed in each plot on 9 December 2007, about 5 weeks before rainfall simulation. We have been monitoring changes in echidna pits in the area for the past 2 years and constructed

our pits to resemble, as closely as possible, natural pits in the area. Natural foraging pits are generally circular-shaped, averaging about 22 cm across, 7–15 cm deep and surrounded by a small accumulation of loose, generally aggregated soil clods (Eldridge and Mensinga, 2007). Pits were constructed 22 cm in diameter and 10 cm deep, and the ejecta soil was deposited in an arc around the perimeter of the pit, mainly on the downhill side, simulating natural pits where the ejecta tends to accumulate downslope. The disturbed soil in the pits (and associated mounds) was allowed to settle; as we were interested in examining how newly constructed pits about 1–2 months old would influence hydrological processes. The five treatments were: control (no disturbance in the plot), one pit (∼5% cover of pits and 7% cover of mounds), two pits (10% pit, 12% mound), four pits (15% pit, 25% mound) and six pits (20% pit, 27% mound). Thus, a plot with six echidna pits had 47% cover of disturbed soil.

Rainfall simulations

Each runoff plot was bordered by sheet steel buried 5 cm into the soil and rising 10 cm above the soil. This prevented water from leaving the plot and was high enough to prevent water falling outside the plot from entering the measuring flume. Runoff was collected in a flume at the lower end of the plot. The flume was constructed so that runoff and sediment would enter from upslope but rainwater was prevented from entering directly from above. Rainfall was simulated on all 25 plots in January 2008. A Morin-type revolving disc rainfall simulator (Grierson and Oades, 1977) was used to apply rainfall to each of the plots. On level terrain the simulator nozzle is calibrated to deliver raindrops from a standard height of 2·05 m, producing rainfall of 2·5 mm diameter mean drop size with energy of approximately 30 kJ m^{-2} min^{-1} using 52 kPa pressure. Rainfall intensity, however, varied slightly between plots due to slight differences in heights between the rainfall nozzle and the ground. The average rainfall intensity of 41·1 mm h^{-1} on any plot varied between 44·3 mm h^{-1} and 39·7 mm h^{-1} (SD = 1·04 mm h^{-1}). Rainfall was applied at a constant rate until steady-state runoff was achieved, usually within 30 min.

Time to ponding and time to runoff were recorded for each plot. Time to ponding is defined as the time elapsed from the commencement of rainfall for free water to cover about 60% of the soil surface. While this method may appear subjective, comparisons with the tensiometer method indicated no appreciable differences between both methods (I. Packer, unpublished data). Furthermore, our technique of estimating time to ponding means that there is no disturbance to the soil surface, which would otherwise occur when using tensiometers. Once time to ponding occurred, a vacuum pump was switched on, pumping any water collecting in the trough (flume) at the lower end of the plot into a measuring cylinder. Time to runoff was defined as the time when the runoff rate

exceeded 5% of the rainfall rate (Giordanengo *et al.*, 2003). Runoff samples were bulked at 5-min intervals, and sediment mass determined after drying at 105 °C for 24 h. Sediment concentration is expressed as mass per litre of runoff. Sediment collected from the plots represents the total contribution from rainsplash and flow-driven erosion processes.

Pit volume was assessed three times during the study up to 27 weeks after simulations. The volume was calculated using the formula for a half of a prolate sphere, and the mass of accumulating sediment calculated by using the values of bulk density for a range of infilling pits found in this study area.

Seed movement during rainfall

Seeds of narrow-leaved hopbush (*Dodonaea viscosa*), a common woodland shrub, were collected from live plants and dried over 3 months in cold storage. Primary dispersal of *Dodonaea* is by ants, but substantial secondary dispersal occurs through runoff. Seeds were painted with a unique combination of different coloured dots. The colour and number of dots indicated their pre-simulation position on the plot, i.e. pit or surface (non-pit). We placed an 8 cm × 8 cm grid across each 0·64 m^2 plot to record the exact seed location. Before each simulation event, seeds were placed in predetermined positions, depending on the number of pits in that plot, and after each simulation, plots were searched to retrieve as many seeds as possible. Their final post-simulation location was recorded on the grid. Seeds that ended up in the flume were recorded as ending up on the surface. Thus, seeds that commenced in a pit had four possible fates: remaining in the same pit (no movement), move to a different pit, move to the surface or lost. Seeds that commenced on the surface had three possible fates: moving to a pit, remaining on the surface or lost. We used the Euclidean distance between the starting and final locations as a measure of the distance travelled by each seed, although we accept that in some cases, their exact trajectory of movement may have been more tortuous.

Statistical analyses

We used a two-way analysis of variance (ANOVA) with five treatments by five blocks to examine differences in hydrological properties, time to ponding (TP), time to runoff (TR) and steady-state infiltration (SSI), and tested for significance between treatments using the block by treatment interaction as the residual mean square (df = 16). Data subjected to ANOVA were first checked for homogeneity of variance using Levene's test and diagnostic tools within the Minitab (2007) statistical programme and transformed, where necessary, to stabilize the variance before undertaking ANOVA. Fisher's Protected Least Significant Difference (LSD) test was used to determine significant differences between means, and where appropriate, Bonferroni tests were used to guard against Type I errors.

The fate of seeds was assessed by calculating the number of seeds recovered from a given microsite, as a

percentage of those that started in a particular microsite. For example, the percentage of pit-commencing seeds retrieved from a different pit was calculated as the number retrieved from the different pits (summed over all five replicate simulations) expressed as a percentage of the total number that started in a pit (minus the number that could not be relocated, i.e. lost seeds). Therefore, if 95 seeds started in a pit, 7 were found in a different pit, 11 were lost altogether (therefore, 84 recovered) and the 'pit to different pit' value would be calculated as 7/100 × (95−11) = 8·3%.

RESULTS

Ponding and runoff

Water ponded on all soils within 1·8 min of commencement, and runoff commenced within about 6·5 min or after about 4·4 mm of continuous rainfall at an average rainfall intensity of 41 mm h^{-1} on the control and 1-pit plots. Runoff commenced significantly later on the 4- or 6-pit plots compared with the other treatments ($F_{4,16} = 16·7$, $P = 0·002$; Table I). Steady-state runoff rate was about 40 mm h^{-1} across the five treatments, reinforcing the notion that these crusted interspace soils have exceptionally low rates of infiltration. The steady-state runoff rate established within 20 min of simulations, but slightly earlier (by 3–5 min) on the control plots (Figure 1). In general, there were no differences in the steady-state runoff rate, the time taken to achieve steady-state runoff or the percentage of rainfall occurring as runoff (runoff coefficient) between the five treatments (Table I). Not surprisingly, however, the rate of increase in runoff over time was greatest on the control plots, least on the 1-, 2- and 4-pit treatments and intermediate on the most-disturbed treatment ($F_{4,16} = 4·74$, $P = 0·018$ on log$_{10}$ ($x + 1$)–transformed data).
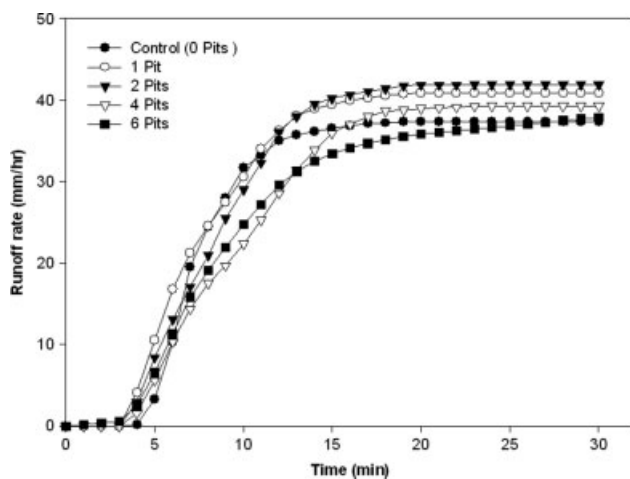

Figure 1. Runoff rates (mm h^{-1}) for the five treatments over 30 min of simulations at an average rainfall intensity of 41 mm h^{-1}. Curves are averaged over the five replicate blocks in each treatment.

Sediment yield

Final cumulative sediment yields ranged from 32 g soil l^{-1} runoff for the control and 1-pit treatments, 44 g soil l^{-1} runoff on the 2- and 4-pit treatments, to 65 g soil l^{-1} runoff for the 6-pit treatments (Figure 2). The rate of sediment removal (g soil l^{-1} runoff min^{-1}) increased with increasing disturbance (Table II) and sediment yield rates for the most-disturbed plots were significantly greater than that for the other plots ($F_{4,16} = 4·77$, $P = 0·010$ on $\sqrt{}$-transformed data).

The trend in relation to the intercepts of the cumulative sediment removal curves was ill-defined (Table II), although the smallest intercept was for 6-pit treatment, possibly suggesting that this most-disturbed treatment had the greatest loss of sediment from the plots during the early stages of simulations ($F_{4,16} = 10·06$, $P < 0·001$ on $\sqrt{}$-transformed data).

An increase in the total cover of disturbance, i.e. increasing cover of pits plus mounds, was associated with substantial increases in sediment concentration ($F_{1,23} = 6·73$, $P = 0·016$, $R^2 = 0·19$). Excluding data from one of the five control plots that for an unknown reason had four times greater sediment yield than the other replicates, increased the explanatory power of disturbance substantially ($F_{1,22} = 18·9$, $P < 0·001$, $R^2 = 0·44$; Figure 3). Based on measurements of the volume and bulk density of soil, the average rate of soil deposition over a 27-week period was $4·46 \pm 0·66$ (mean $\pm$ SEM) g soil day^{-1}. Pit volume declined from $1880 \pm 10·3$ cm^3 (mean $\pm$ SD) to $729 \pm 3·4$ cm^3 (mean $\pm$ SD) within 6 months of rainfall simulations.

Seed fate and movement

We retrieved 180 seeds after the simulations or 82% of all seeds. Retrieval rate tended to increase with reductions in pit density as most seeds ending up in pits were found in the sediment at the bottom of the pits. Pit-to-pit movements tended to increase, while pit-to-surface movements tend to remain unchanged with increasing disturbance (Table III). Surface-to-surface movements were ill-defined, and surface-to-pit movements tended to increase with increasing disturbance (Table III).

There were two general trends in relation to the distances that seeds moved. Generally, for seeds remaining on the surface, there was a reduction in the distance that they travelled, from 33 to 18 cm, with increasing disturbance (Figure 4). For seeds moving from the pits to the surface (9·5% of all pit movements), the distance that they moved declined sharply with increasing disturbance.

DISCUSSION

This study describes how the foraging activities of the echidna, a ubiquitous woodland engineer, influenced a number of key biotic and abiotic processes in woodlands. Disturbance of the biologically crusted matrix soils by echidnas produced surface detention storages sufficient to retard the onset of runoff by up to 3 min, doubled

Table I. Mean values of hydrological properties in relation to the five treatments.

Hydrological property	Treatment (number of pits)				
	0	1	2	4	6
Time to ponding (min)	1·69[a]	1·75[a]	1·74[a]	1·71[a]	1·50[a]
Time to runoff (min)	7·76[a]	6·67[a]	8·50[a]	11·66[b]	11·75[b]
Steady-state runoff rate (mm h^{-1})	39·88[a]	40·86[a]	41·92[a]	39·27[a]	38·56[a]
Time to steady-state runoff (min)	14·10[a]	17·00[a]	19·80[a]	18·80[a]	18·60[a]
Rate of change in RO (mm min^{-1})	8·47[a]	4·26[b]	4·17[b]	5·74[b]	5·85[ab]
Runoff coefficient (%)	63·0[a]	56·0[a]	60·0[a]	58·0[a]	48·0[a]

For a given hydrological property, different superscripts indicate significant differences at $P < 0.05$.
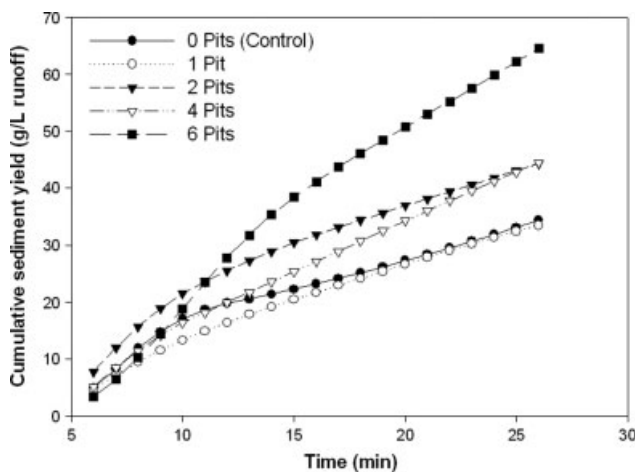RO represents runoff; runoff coefficient is runoff expressed as a percentage of applied rainfall.

Figure 2. Cumulative sediment yield (g l^{-1} runoff) for the five treatments.

the rates of sediment removal and trapped seed. Pits could therefore be considered filters (*sensu* Noordwijk van *et al*., 2004) in the sense that they have the capacity to interfere with lateral flows of water, soil and biotic material entrained within such flows. Our data are consistent with the notion that pits are important repositories of seed (Isselin-Nondedeu *et al*., 2006) and support previous research showing that the ejecta mounds, the structures resulting from surface disturbance, are substantial sources of rainsplash-eroded sediment, particularly under conditions of sparse plant cover (Imeson and Kwaad, 1976; Sherrod and Seastedt, 2001). Taken together, the results of this study support the contention that foraging by echidnas provides a mechanism for assembling, in space, three critical resources, water, sediment and seed, which are all critical for the functioning of arid and semi-arid ecosystems (Whitford, 2002). Foraging by

echidnas therefore has important implications for the maintenance of functional ecohydrological processes in semi-arid woodlands.

Crust removal by foraging increases erodibility and runoff

The greatest levels of soil disturbance (6-pit treatment; ~47% surface disturbance) resulted in sediment removal rates twice that of adjacent undisturbed surfaces (64 cf. 32 g soil l^{-1} runoff, respectively). We attribute increases in sediment removal with increasing disturbance to changes in the cover of mounds, through greater removal of the soil crust, and to a lesser extent, exposure of subsoil after pit excavation. Biological soil crusts that dominated the inter-pit matrix are resistant to water and wind erosion due to the presence of extracellular polysaccharides and gels in their surface layers (Hill *et al*., 1997). Surface disturbance by echidnas disrupts these cementing agents, converting erosion-resistant macroaggregates to erodible microaggregates and effecting a state change from an erosion-resistant state to one that is highly erodible by water (Mucher *et al*., 1988; Yair, 1995; Eldridge and Greene, 1994; Eldridge, 1998). The result is a patchwork of highly erodible pit and mound microsites nested within a non-erodible matrix of soil crust. In their undisturbed state, biological soil crusts have low rates of hydraulic conductivity and therefore high rates of runoff (Eldridge *et al*., 2002). Consequently, runoff coefficients were extremely high, particularly on the least-disturbed treatments.

In the context of animal foraging pits, the extent to which surfaces will erode likely depends on the size of disturbances and their spatial configuration. Sediment loads in this study increased with increasing density of foraging pits, consistent with observations of pits created

Table II. Slopes and intercepts of the regression lines of cumulative sediment yield against time.

Attribute	Treatment (number of pits)				
	0	1	2	4	6
Slope of curve	1·26[a]	1·37[a]	1·65[a]	1·87[a]	3·05[b]
Intercept of curve	6·90[ab]	3·87[bc]	8·88[a]	4·14[bc]	3·08[c]

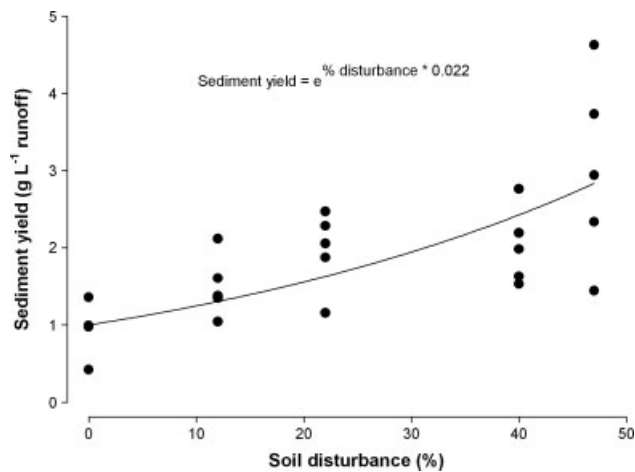For a given attribute, different superscripts indicate significant differences at $P < 0.05$.

Figure 3. Sediment yield (g soil l^{-1} of runoff water) in relation to total cover of disturbances at the site. One value for the control plot (4·00 g soil l^{-1}) has been omitted from the plot.

Table III. Fate of *D. viscosa* seeds (%) for pit and surface movements.

Fate of seeds	Treatment (number of pits)					Total
	Control	1	2	4	6	
Pit movements						
Pit to different pit	0·0	0·0	1·2	1·2	8·3	10·7
Pit to same pit	0·0	9·5	21·4	17·9	31·0	79·8
Pit to surface	0·0	1·2	1·2	3·6	3·6	9·5
Surface movements						
Surface to pit	0·0	0·0	1·0	5·2	14·6	20·8
Surface to surface	24·0	8·3	13·5	9·4	24·0	79·2

Data have been adjusted to account for seeds that could not be retrieved.
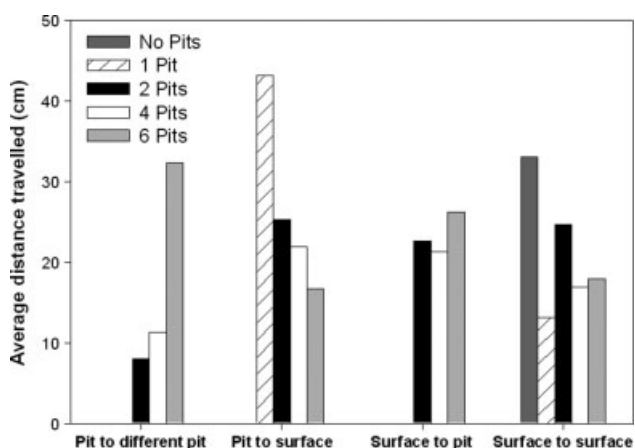

Figure 4. Average distance travelled (cm) by *D. viscosa* seeds for the five treatments in relation to their fates. Seeds that remained in the same pit have not been included because they are not considered to have travelled any distance.

by heteromyid rodents in shrub-encroached arid grassland (Neave and Abrahams, 2001). Unlike landscape-scale erosion processes, sediment generated from animal disturbances is unlikely to move large distances, largely because sediment loads are generally small, and

the mounds, grass tussocks and other forms of vegetation barriers mitigate against off-site removal. Reports of splash erosion from pocket gopher (*Thomomys talpoides*) mounds indicate that sediment moves less than 50 cm from the source because it is trapped by mounds further downslope (Sherrod and Seastedt, 2001).

Seed dispersal and capture

Relatively few studies have documented the importance of animal-produced pits and depressions as sinks for seed (Rotundo and Aguiar, 2004; James and Eldridge, 2007). Seed capture can result from wind-driven processes (James *et al.*, 2009) or water deposition (Cerda and Garcia-Fayos, 2002), and in this study, relatively high levels of runoff from the biologically crusted surfaces provided the mechanism for seed movement (hydrochory). The extent to which seeds move likely depends on factors such as seed mass and shape, depth of sheet flow and spatial arrangement of surface obstructions. The few studies considering seed removal by rainfall suggest a tendency for a few large rather than many relatively small movements (Isselin-Nondedeu *et al.*, 2006). While we retrieved some seeds outside the plot, which had obviously moved by splash erosion, the plot size in our study was too small to allow any examination of the relative size of individual movements.

We expected that, as the cover of pits increased, seeds being moved in runoff water would travel shorter distances simply due to the increased likelihood of encountering another pit. It is somewhat counterintuitive, therefore, that seeds splashed from one pit and trapped in another actually travelled greater distance as pit cover increased. One possibility is that as the cover of pits and their associated mounds increased, corresponding with a reduced area of inter-pit matrix, the same volume of overland flow would need to travel across a smaller surface area. Flow across the surface would therefore be deeper and stronger and along a more tortuous path than a surface with fewer disturbances. On the contrary, seed movement in areas of slow moving, shallow sheet flow (i.e. control, 1- and 2-pit plots) would likely have been through water droplets 'bouncing' the seeds along the ground, analogous to processes of splash erosion (Aerts *et al.*, 2006). Consequently, seeds would have been dispersed shorter distances. The bounding movement of seeds by rain drops is likely to be greater at the commencement of rainfall when the soil is dry and when splash erosion processes predominate (Garcia-Fayos and Cerda, 1997). Seeds remaining on the surface generally travelled shorter distances, from 33 to 18 cm, with increasing disturbance, but the results were inconclusive and difficult to account for.

Notwithstanding the observations of greater dispersal distances with increasing disturbance, a substantial effect of mounds is to increase the tortuosity of flow and thus potentially increase the chance that seeds will become entrapped within a pit or within a plant tussock (Day and Wright, 1989; Cabin *et al.*, 2000). Pits and depressions

may favour particular dispersal modes or seed types such as weedy, wind-dispersed and therophytes (Milton *et al.*, 1997; Isselin-Nondedeu *et al.*, 2006). Only one species of seed was used in this study, however, and the relative effect of runoff water on seed movement may well have been different had different shaped seeds or those with appendages or mucilaginous secretions been used (Cerda and Garcia-Fayos, 2002; Isselin-Nondedeu *et al.*, 2006). Observations of natural seed germination in pits in this study area show that they support substantially more germinants that adjacent non-pit surfaces, but the extent to which they enhance plant survival is largely unknown.

Echidna pits and the maintenance of functional woodlands

Foraging by echidnas breaks open the soil crust, creating sinks for water, soil, seed and organic matter within an extensively crusted matrix of low hydraulic conductivity. Although foraging pits in this study were of similar size and regularly spaced, under natural woodland conditions they range from shallow nose pokes (30 cm^3) to expansive areas of surface scraping (up to 7000 cm^3; Rismiller, 1999; Eldridge and Mensinga, 2007; Eldridge and Kwok, 2008). The pattern of ponding under natural rainfall would therefore likely vary across the plots, with deeper ponds in the larger pits adjacent to shallow, intermittent ponds in the smaller scratchings, and dry inter-pit surfaces dominated by biological soil crusts. Even small gaps in the crust could act as microsinks, mimicking the pattern evident at larger scales, particularly where hydrophilic mosses occur adjacent to hydrophobic lichens (Bowker *et al.*, 2010). The balance between erosion and deposition likely changes over time (*sensu* Imeson and Kwaad, 1976) as echidnas excavate new pits and reactivate old pits located in resource-rich area patches such as termite pavements (Noble *et al.*, 1989) or ant nests (Abensperg-Traun and De Boer, 1992; Rismiller, 1999). Pits function as resource traps until they infill over a period of about 2 years by aeolian- and water-borne processes (D.J. Eldridge, unpublished data). In this study, pit volume declined by 63% within 6 months of rainfall simulations with an average accretion rate of 4·5 g soil pit^{-1} day^{-1}.

The results of this study suggest that echidna foraging pits have a resource coupling role; bringing together water, seed and eroded soil, initiating the formation of resource-rich hydrophilic patches within a largely crusted hydrophobic matrix. Echidna pits soils are moister, even after extensive dry periods (Eldridge and Mensinga, 2007), simply because water percolates deeper into the soil profile and is less likely to evaporate. The combination of a greater amount of pit-trapped seed and capture of eroded soil helps to trap litter in the pits (James and Eldridge, 2007), enhancing the breakdown process by bringing microbes into contact with organic matter. Because pits act as filters and retain resources *in situ* at fine spatial scales within runoff zones, their effect may be to uncouple runoff slopes from drainage lines,

analogous to the trapping of water and sediment by arid zone vegetation (Tongway, 1990).

The study has identified the extent to which echidna-created filters modify the rate of coupling of resources entrained in lateral flows. If this is the case, then the location of these pits is as important, if not more important, as the total area they occupy (Noordwijk van *et al.*, 2004). Unlike perennial vegetation, however, echidna pits are relatively small and therefore go largely unnoticed by land managers. The extent of both foraging pits (filters) and resource flows (water, soil, seed; flows) gives us insights into the extent to which resources are captured or lost in the semi-arid woodlands. Understanding the balance between resource capture and retention will be critical to improving our understanding of the ecohydrological significances of soil foraging animals such as echidnas.

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