PROCEEDINGS OF THE AUSTRALIAN RANGELAND SOCIETY BIENNIAL CONFERENCE

Official publication of The Australian Rangeland Society

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Form of Reference

The reference for this article should be in this general form; Author family name, initials (year). Title. *In*: Proceedings of the nth Australian Rangeland Society Biennial Conference. Pages. (Australian Rangeland Society: Australia).

For example:

Anderson, L., van Klinken, R. D., and Shepherd, D. (2008). Aerially surveying Mesquite (*Prosopis* spp.) in the Pilbara. *In*: 'A Climate of Change in the Rangelands. Proceedings of the 15th Australian Rangeland Society Biennial Conference'. (Ed. D. Orr) 4 pages. (Australian Rangeland Society: Australia).

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ECHIDNAS (TACHYGLOSSUS ACULEATUS) AS WOODLAND ENGINEERS

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ABSTRACT

Many animals create soil surface disturbances (biopedturbation) while constructing habitat, foraging for food or excavating resting sites. We studied the effects of foraging pits of the Short-Beaked Echidna (*Tachyglossus aculeatus*) on soil biota and biogeochemistry. Echidna foraging pits trapped more litter, were moister and cooler. Pit soils were more porous, and had greater levels of sorptivity and steady-state infiltration. Pit soils had greater levels of electrical conductivity but lower concentrations of C, N and S. Soil micro-arthropods were more abundant in the pits, and had a different composition to those on the surface. Pits had greater rates of microbial respiration. Our results indicate that echidnas are important ecosystem engineers, and contribute to the maintenance of small-scale patchiness in semi-arid woodlands.

INTRODUCTION

Arid and semi-arid landscapes function most efficiently when essential resources (e.g. water, nutrients, organic matter, seed) are concentrated into discrete patches. This patchiness exists at a range of spatial scales, and the functionality of the landscape is highly dependent on the maintenance of this patchiness. A major contributor to this spatial heterogeneity is soil disturbance by animals (biopedturbation; Whitford and Kay 1999). Soil biota 'engineer' the environment, maintaining, creating or modifying habitat by controlling the availability of resources to themselves and/or other organisms without actually consuming these resources ('ecosystem engineers' Jones *et al.* 1994).

A widespread form of animal-moderated soil engineering in eastern Australia is the mosaic of pits and scrapings created by the Short-Beaked Echidna (*Tachyglossus aculeatus*), which it creates while foraging for epigeal invertebrates. During foraging, echidnas rake over the ground and excavate shallow digs, aerating the soil, and displacing a large volume of sediment. A recent study in eastern Australia demonstrated that echidnas excavate in excess of 7 t/ha of soil while foraging (Kwok 2005).

Given the extensive continental distribution of echidnas and their soil turnover (Rismiller 1999), we predicted that their diggings would have a substantial effect on the creation of small-scale patchiness by altering the chemistry and biology of surface soils. Specifically, we predicted that echidna pits would trap and store more litter, be moister and cooler, accumulate soil with greater concentrations of carbon (C) nitrogen (N), phosphorus (P) and sulphur (S), have greater infiltration rates, higher soil respiration rates, and therefore support a more diverse and abundant micro-arthropod community, compared with non-pit soils.

METHODS

The study was conducted within a *Eucalyptus intertexta-Eucalyptus populnea* open woodland at Yathong Nature Reserve, near Cobar in western NSW. We selected seven sites separated by about 500 m. At each site we examined pits and adjacent non-pits under the canopies of two tree species (*Eucalyptus* sp., *Alectryon* sp.), and pits and non-pits out in the open. Thus, for each of the seven sites, there were two tree types by two canopy treatments by two pit treatments, resulting in 56 sample locations. All pits were of a similar age and morphology.

Surface soil was collected from each sample location and analysed for soil moisture, bulk density, total N, S and C, extractable P, pH, electrical conductivity (EC) and active C. Soil respiration was measured on soils in the laboratory (Anderson 1982). Water flow through the soil (sorptivity and steady-state infiltration) was measured using disc permeameters at a supply potential of +10 mm (ponded). We measured ambient temperature, and the temperature above and below the litter at all sites with a laser thermometer, and the mass of total litter and its components (leaves, bark etc). Intact cores of soil and litter samples were collected to extract micro-arthropods using tulgren funnel over a 7 day period. Micro-arthropods were classified according to Order, and enumerated.

Soil physical and chemical data, litter mass, infiltration and temperature were analysed using a nested design ANOVA with multiple error terms. Multi-variate analyses were used to examine patterns in diversity and abundance of soil micro-arthropods.

RESULTS

Pits trapped more than twice the mass of litter (37.2 g - pit, 18.0 g - surface), comprising more bark and leaves, compared with non-pits. The increase in litter mass in pits was greater in the open compared with under the canopy. Larger pits tended to trap more litter. Electrical conductivity was greater in the pits (0.07 dS/m compared with 0.06 dS/m), and the concentrations of total C, N and S were significantly lower in the pits. In general, the decline in nutrients from surface to pit was greater under the canopy compared with out in the open. Interestingly, changes in litter mass in the pits did not account for differences total C, N, or S, active C or P.

Pit soils were less dense (1.22 Mg/m³ compared with 1.36 Mg/m³), pits were significantly moister (1.7 % compared with 1.1%) and temperatures below litter in the pits was significantly cooler (by 2.2° C) than in the non-pits. Microbial respiration was about 30% greater in the pits compared with the surface. Sorptivity and steady-state infiltration were about twice that in the pits (353 mm/h^{0.5}, 76 mm/h) compared with the surface (192 mm/h^{0.5}, 38 mm/h, for sorptivity and infiltration respectively).

Less than 20 individual micro-arthropods were extracted from litter. However, for microarthropods extracted from soil, there were clear differences in the composition between pit and surface microsites. Mites (Acari) were the most abundant group, and accounted for 74% of the dissimilarity between pit and surface microsites. Micro-arthropods were more abundant in the pits (107 compared with 30), and more Orders were detected in pits (4.4 compared with 3.3).

DISCUSSION

In this semi-arid woodland, echidna foraging pits captured substantial amounts of organic matter, altering soil biogeochemistry and providing habitat for soil micro-arthropods. Pits trapped twice the mass of litter compared with non-pit surfaces. Litter is known to moderate

fluctuations in soil temperature and reduces losses in soil moisture (Zaady *et al.* 1996) and lower temperatures would increase the period over which litter-active micro-arthropods remain above-ground before retreating into the soil as temperature increases (Cepeda-Pizarro and Whitford 1989). Reduced evaporation resulting from lower temperatures would increase the period over which soil moisture is optimum for microbial decomposition of organic matter (Whitford 2002). Further, the observed higher rates of respiration in the pits suggests to us greater microbial and micro-arthropod abundance in the pits (e.g. Ayarbe and Kieft 2000). Pits, irrespective of shape and size, will hold litter *in situ* more effectively than if it remains on the soil surface (Whitford 2002). If this litter is covered by soil, as occurs through subsequent animal disturbance, wind or water erosion, decomposition is likely to be greater, resulting in enhanced mineralisation.

We attribute greater infiltration in the pits to the greater number of macropores; biopores > 0.84 mm in diameter, that are created by invertebrates and plant roots and predominate close to the canopies of large trees. Echidna digging would also have destroyed the largely hydrophobic biological soil crust, reducing runoff from the crust, exposing surface macropores, and resulting in greater levels of infiltration. Pit soils were also more porous, most likely due to the direct effects of digging, greater litter incorporation and greater abundance of soil organisms (Lee and Foster 1991).

Lower concentrations of N were detected in the pits, contrary to studies that report increased nitrogen in animal-created pits (Whitford and Kay 1999, Eldridge and Rath 2002). Litter is a sink for mineralised nitrogen, and while nitrogen accumulates in litter during the early phase of decomposition, it is not released until the latter stages. Coarse litter in the pits probably resulted in N immobilisation during decomposition, a consequence of high C to N ratio. This likely explains the lower levels of nitrogen in the pits.

Most micro-arthropods in our study were extracted from soil. While micro-arthropod richness varied little between pits and surface soils, it was greater under the tree canopies, and increased with increasing litter mass. This suggests to us that the pits in our study, which were all of a similar age and size, may not be providing the necessary range of habitats required for a diverse community of litter-dwelling micro-arthropods. Older or larger pits, or pits further from the canopy in areas of greater solar radiation, would provide a greater arrangement and distribution of litter of varying size and in varying stages of decomposition, resulting in a more variable distribution of soil biota in semi-arid systems.

At the landscape scale, echidna foraging created a mosaic of pits in different stages of development and recovery, similar to that observed for other soil foraging animals (e.g. bettongs; Garkaklis *et al.* 2003). Parallel studies indicate a greater density of echidna pits close to the canopies of large Eucalypts (Kwok 2005). We anticipate that pits found in the open would trap more groundstorey plant litter rather than coarse woody material from the trees, resulting in lower C to N ratios in the soil and therefore greater levels of available nitrogen. We predict therefore that strong positive feedback processes will operate under tree canopies as pits increase soil nutrients, in turn increasing plant growth and water accumulation and therefore habitat for soil organisms. Ultimately these processes result in greater food resources for echidnas, stimulating further foraging. Increased litter capture influences populations of soil fungi and affects patch-level processes such as recruitment and survival of seedlings (Whitford and Kay, 1999), and landscape-level processes such as the distribution and availability of essential resources.

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