DISTURBANCE BY ANIMALS AT VARYING SPATIAL SCALES IN A SEMI-ARID AUSTRALIAN WOODLAND

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ABSTRACT

We studied soil disturbance by rabbits, echidnas, goannas, ants and termites at three spatial scales across four vegetation communities (dense woodland, open woodland, shrubland, grassland) in a semi-arid rangeland in western NSW. Bare and litter-covered surfaces (microscale) were nested within canopy and open patches (intermediate scale), which were nested within vegetation communities (landscape scale). Differences in disturbance measures (cover, soil excavation) between vegetation communities varied depending on the scale of disturbance and the scale at which the disturbance was measured. Our study documents the extent of animal activity in semi-arid woodlands and reinforces the notion that, as soil disturbance is scale-dependent, differences between species, habitats and communities will depend on the scale at which disturbances are examined.

INTRODUCTION

Semi-arid and arid environments are typically patchy. Resources are distributed into 'fertile islands' (Garner and Steinberger 1989), which are patches of higher soil fertility, moisture, plant productivity and animal activity. These patches are initiated and maintained by abiotic and biotic processes of resource distribution. Such processes operate within a hierarchy of scales, with processes at smaller scales affecting those at higher levels of organization.

Animal-soil disturbances are important for maintaining this patchiness. Disturbances made while foraging or creating resting sites can change soil physico-chemical properties by altering water infiltration (Jackson *et al.* 2003), nutrient distribution and a range of other soil properties (Whitford and Kay 1999). 'Pits' trap resources, increasing plant productivity at landscape scales (e.g. Boeken *et al.* 1998).

Research on soil disturbance by animals in Australia has focused on the physical and ecological effects of ground-foraging animals. Disturbances that have significant ecological effects include the foraging digs of woylies (*Bettongia penicillata*) (Garkaklis *et al.* 2003), echidnas (*Tachyglossus aculeatus*) (Eldridge and Mensinga 2007), the greater bilby (*Macrotis lagotis*) (James and Eldridge 2007), and the resting forms of kangaroos (Eldridge and Rath 2002).

The aim of this study was to investigate the soil disturbance by woodland-active animals among four vegetation communities at three spatial scales. We tested four predictions: (1) the magnitude of animal disturbances (i.e. cover and density of disturbances, mass of excavated soil) at intermediate scales is greater under tree canopies compared with open patches, (2) the level of animal activity and therefore the number and magnitude of disturbances, increases with increases in tree density (3) the spectrum of animal disturbances varies between vegetation communities, and (4) the density and cover of fine-scale disturbances (ant and termite cartons) is independent of vegetation community.

METHODS

Location and experimental design

This study was conducted at Yathong Nature Reserve south of Cobar (32°37'S, 145°34'E) in west-central NSW within four vegetation communities ranging in cover and complexity: dense *Eucalyptus intertexta*- *Callitris glaucophylla* woodland, open *E. intertexa*, *E. populnea* woodland, Acacia and Senna shrubland, and perennial grassland (*Stipa* spp.). Rainfall at Yathong averages 330 mm per year but is highly variable. Animals create soil disturbances of different sizes at different scales. At the landscape scale, European rabbits (*Oryctolagus cuniculus*) construct warrens (or occupy warrens of locally-extinct bettongs *Bettongia lesueur*) that cover several hundred square metres. At intermediate scales (metres), goannas (*Varanus gouldii*, *V. varius*) and echidnas (*Tachyglossus aculeatus*) dig foraging pits, and kangaroo (*Macropus giganteus*, *M. fuliginosus*, *M. rufus*) excavate shallow depressions for resting. At the finest (microsite) scale (centimeters), ants (*Rhytidoponera* spp., *Camponotus* spp.) and termites (*Drepanotermes* spp.) excavate burrow entrances and excrete decomposed cellulose to form cartons or pavements (Noble *et al.* 1989).

Four 25 ha sites were surveyed in each community. Rabbit warrens were counted within the entire site, while intermediate-sized disturbances (echidna, goanna, kangaroo digs) were sampled within three sets of 10 m x 10 m plots centred on a mature Eucalyptus canopy and paired with an adjacent open plot. The smallest disturbances (ant, termite) were recorded within three pairs of 0.5 m x 0.5 m quadrats within each 10 m x 10 m plot, one on a litter surface and one a bare surface. We recorded the dimensions and animal responsible for each disturbance and used these measurements to calculate cover of disturbances and mass of excavated soil.

Differences in rabbit warrens between the vegetation communities were tested using one-way ANOVA. Intermediate-sized disturbances were scaled up to the landscape scale by adjusting for the density of large trees at each site. Mixed model ANOVA was then used to test for differences in density, soil excavation and cover of disturbances in relation to communities, patch type (canopy/open) and their interactions. Microsite-scale data were similarly analysed, but included a stratum for microsite (litter/bare). Post-hoc differences in means were compared using LSD tests.

RESULTS

There were six-times as many warrens in the open woodland, and three-times as many in the shrublands compared with the dense woodland ($F_{3,8}$=5.69, P=0.022). Warren soil mass per hectare was significantly greater in the grasslands compared with the dense woodlands and shrublands ($F_{3,8}$=3.79, P=0.059), due to their generally larger size.

Echidna and kangaroo disturbances dominated under the canopy, while echidna and goanna disturbances were co-dominant in the open (Fig. 1a). Termite pavements were more abundant in the open, while kangaroo hip holes were largely absent from open areas (Fig. 1a). There were four times more disturbances under the canopies (19.4 per 100 m^2 canopy) compared with a similar area in the open (3.8; $F_{1,16}$=38.8, P<0.001, Fig. 1a). There was 10-times greater cover (P<0.001) and 30-times greater soil mass ($F_{1,16}$=62.5, P<0.001) under canopies compared with in the open. At the level of the canopy/open, there were no differences between communities in density, cover or mass of soil disturbances.

Scaling intermediate-sized canopy/open disturbances up to the landscape scale revealed that disturbances were marginally more abundant in the dense and open woodlands (690-905 disturbances /ha respectively) compared with either grasslands or shrublands (235-238 disturbances/ha; $F_{3,8}$=3.95, P=0.05, Fig. 1b). When added together, total soil mass by all animals was similar, ranging from 0.49 t /ha for grassland to 2.77 t/ha for dense woodland. Despite the importance of tree canopies as focal points foraging, we found no significant relationships between increasing density of trees at the landscape scale and density, cover or mass of soil disturbances (P>0.27).

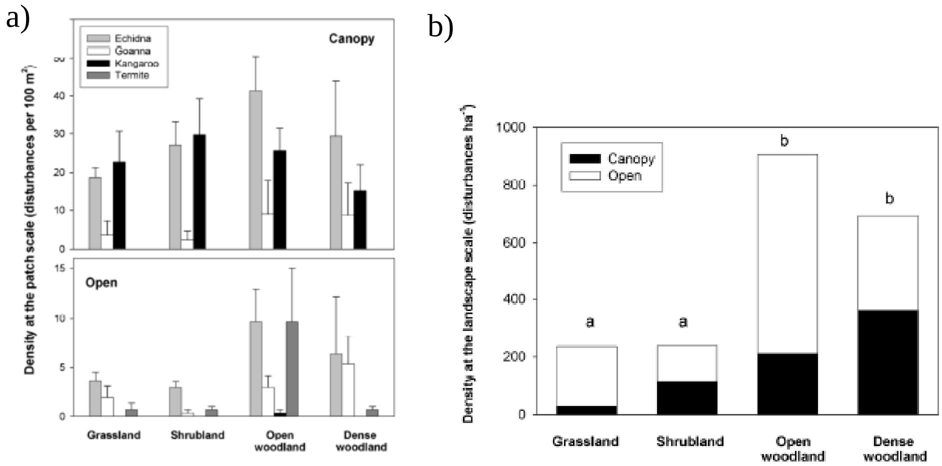

Figure 1. Mean (+ SE) density of intermediate-sized disturbances a) within the 100m^2 canopy and open patches. Note different scales on y-axis for canopy and open and, b) when scaled up to the landscape scale. Different letters indicate a significant difference in disturbance at *P*<0.05.

The only significant differences in microsite-scale disturbances were 1) larger area of surface disturbances by ants and termites in open woodland ($F_{3,8}$=4.28, P=0.04) and 2) seven-times greater disturbances on litter-dominated (0.06%) compared with bare (0.008%) surfaces ($F_{1,3}$=24.67, P<0.001). There were no significant effects of community or patch type on density or cover.

DISCUSSION

Our study demonstrated marked differences in the patterns of soil disturbance at the three spatial scales. As predicted, there were substantially more intermediate-sized disturbances beneath tree canopies compared with open areas. When scaled up to the landscape scale, however, results for these disturbances indicate that open areas are substantial contributors to landscape-scale soil disturbance, particularly in communities where open patches make up a considerable proportion of the landscape. However, this scaling also demonstrated that disturbances below the canopy contributed disproportionately to both total density and soil excavation at landscape levels. For example, while only 10% of dense woodlands were covered by the canopies of large trees, 63% of the total mass of soil excavated in this community occurred beneath the canopy. We found no support for the hypothesis that animal activity increases as tree density increases across the vegetation communities.

Soil disturbance – a scale dependent phenomenon

This study has demonstrated that the drivers of soil disturbance i.e. the patterns of vegetation that influence the spatial distribution of soil-disturbing animals, are scale- and process-dependent. While landscape-level disturbances (rabbit warrens) varied between vegetation communities, finer-scale disturbances were not. Similarly, intermediate-level patterns of vegetation distribution such as the canopy and open areas were only important for disturbances operating at intermediate scales (echidna, goanna, termite pavement). The importance of vegetation as a driver of soil disturbances in this semi-arid woodland depends on both the scale at which the structure is observed, and the scale of the vegetation driver. Similarly, animal disturbances in the semi-arid woodlands were scale-dependent, with clear preference for the canopy microsites at intermediate scales but not at landscape scales.

The results of this study also suggest that the extent and distribution of soil disturbances by animals, particularly native animals, may be a useful non-invasive method of assessing habitat quality and preference for foraging sites at different spatial scales. For example, Hone (1988) showed that the number of diggings by feral pigs (*Sus scrofa*) was indicative of pig densities. Similarly, our understanding of these preferences at the landscape scale could inform management decisions about which areas are of highest conservation priority. For example, if each landscape (or vegetation community) shows the same trends of increased animal foraging under trees, then those landscapes with few scattered trees may be a greater management priority due to their important habitat significance compared with communities that have many trees. Research is currently underway to establish the nature of the links between foraging activity of woodland animals and resources.

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