

The relationship between animal foraging and nutrient patchiness in south-west Australian woodland soils

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Abstract

The woylie (*Bettongia penicillata*) was once common and abundant over the southern third of the Australian continent. Since European settlement the range of this rat-kangaroo has become reduced by more than 97%, and until the early 1990s, only 3 small natural populations remained, all in south-western Australia. These medium-sized (c. 1 kg) marsupials create a large number of diggings as they forage for the hypogeous fruiting bodies of ectomycorrhizal fungi upon which they feed. The effect of such foraging activity on the availability of plant nutrients in the vicinity of such diggings was evaluated in simulated digging experiments. Available nitrate, ammonium, and sulfur decreased significantly 3 years after diggings were constructed and had filled in, whereas phosphorus, potassium, iron, and organic carbon remained unchanged. The results suggest that preferential water infiltration via woylie diggings leads to a decrease in those soil nutrients that are susceptible to leaching and indicates that digging vertebrates may influence the distribution of surface soil nutrients.

Additional keywords: ectomycorrhizal fungi, biopedturbation, mycophagy, soil heterogeneity, woodlands, soil water repellency.

Introduction

Despite a long recognition that burrowing vertebrates may influence soil characteristics and soil formation processes (Grinnell 1923; Greene and Reynard 1932), few published experiments have quantified this relationship. However, several recent publications have demonstrated the effects of vertebrate digging and burrowing, termed biopedturbation, upon a number of soil properties (Noble 1993; Boeken *et al.* 1995; Garkaklis *et al.* 1998; Alkon 1999; and reviews by Kinlaw 1999; Whitford and Kay 1999). Studies that have investigated biopedturbation by mammals, particularly the effects of burrow mounds, are primarily from North America (see Whitford and Kay 1999), with several studies in southern Africa, Israel (Gutterman and Herr 1981; Gutterman 1997; Alkon 1999), and South America (Whitford and Kay 1999). For example, the impacts on nutrient cycling processes because of the influence of pocket gophers (*Thomomys bottae*) (Mooney and Hobbs 1994), kangaroo rats (*Dipodomys spectabilis*) (Chew and Whitford 1992; Guo 1996), and prairie dogs (*Cynomys ludovicianus*) have all been measured (Carlson and White 1988).

In comparison, very few studies have measured the effects of vertebrate biopedturbation on soil biology in Australia. Noble (1993) showed that large circular features in central Australia with altered distributions of calcrete were probably the result of the warrens of burrowing bettongs (*Bettongia lesueur*), a species of rat-kangaroo absent from the survey area for many decades. Smaller surface soil features with elevated nitrogen and organic carbon levels were the result of mounds constructed by megapode birds (Noble 1993). Ground foraging Australian birds have also been shown to displace soil, resulting in a down-slope movement of the surface soil, in temperate forest ecosystems (Ashton and

Bassett 1997). Resting sites, or hip holes, of kangaroos (*Macropus* spp.) affect the spatial distribution of nutrients because of the accumulation of dung at these sites (Eldridge and Rath 2002). Burrows constructed by varanid lizards (goannas) may influence water infiltration and, hence, the distribution of mulga (*Acacia aneura*) (Whitford 1998). Water infiltration is also affected by the foraging of rat-kangaroos (Garkaklis *et al.* 1998), and can lead to a high degree of heterogeneity in the water repellency of surface and subsurface woodland soils (Garkaklis *et al.* 2000). Introduced pest species have been shown to have detrimental effects on Australian soils. For example, the rabbit (*Oryctolagus cuniculus*) constructs warrens that increase the likelihood of erosion over the disturbance area (Eldridge and Myers 2001).

Digging and burrowing are common behaviours in many Australian mammals, for instance potoroid rat-kangaroos, such as bettongs and potoroos (Claridge and May 1994; Garkaklis *et al.* 1998; Claridge and Barry 2000), bandicoots and bilbies (Strahan 1995), and several species of rodents (Dickman 1999). We examined the effects of mammal foraging on the availability of soil nutrients, using diggings made by the brush-tailed bettong or woylie (*Bettongia penicillata ogilbyi*) as a model. Bettongs are medium-sized (*c.* 1 kg) kangaroo-like marsupials, which feed extensively on the hypogeous fruiting bodies of ectomycorrhizal fungi (Christensen 1980; Seebeck *et al.* 1989; Johnson 1994; Claridge and May 1994). In accessing this food resource, bettongs can make a large number of diggings in the surface soil.

At the time of European settlement, woylies were the most common bettong species in Australia, with a distribution that covered most of the mainland south of the tropics (Troughton 1957; Finlayson 1958; Burbidge *et al.* 1988; Start *et al.* 1995, 1998). At times they reached very high densities and observations of woylies 'swarming' were made in the 1880s (Wood Jones 1925). Indeed, the number of woylies in South Australia in the early 1900s was so high that they were trapped and sold by the dozen for coursing (Wood Jones 1925; Copley 1995).

The distribution of woylies has since declined dramatically. Lomolino and Channell (1995) suggested that the range contraction for all subspecies is 97%. The natural distribution of woylies has now contracted to the most mesic parts of its former range, a pattern of decline similar to that of many small to medium-sized terrestrial mammals in Australia (Burbidge and McKenzie 1989; Start *et al.* 1998). From its original distribution across the south-western third of the continent, it has been reduced 'almost to extinction' (Start *et al.* 1998), and by the early 1990s only 3 relict populations remained in woodlands in the south-west of Western Australia. Conservation measures currently in place for this species include feral predator control, habitat management, and translocation programmes to reserves within Western Australia, and to New South Wales (P. Mawson, pers. comm.) and South Australia (Delroy *et al.* 1986; Short *et al.* 1992; Start *et al.* 1998).

In areas where remnant or translocated populations of woylies occur, the ground is covered in small diggings. Previous studies of the effects of these diggings on soil properties showed that they lead to an increase in water infiltration through preferential flow (Garkaklis *et al.* 1998), that they accumulate organic matter as they decay, apparently promoting the growth of masses of fungal hyphae, and that they become sites of high soil water repellency below the soil surface once they erode and fill (Garkaklis *et al.* 2000). The aim of this study was to measure the effect of foraging on soil nutrients, particularly once the diggings had decayed and disappeared.

Methods

Study site

This study was carried out in Dryandra Woodland (32°48' S, 116°54' E), 200 km south-east of Perth, Western Australia. In this region, mildly dissected slopes that have soils primarily derived from the pre-weathered pallid or mottled zones of the laterite profile, or from unweathered granite separate residual small flat-topped hills. Upper slope soils are shallow and stony, whilst medium- and heavy-textured red earths occur on the mid-slopes (McArthur *et al.* 1979). Soils in the study site are typically Gn2.15 according to Northcote (1979).

Dryandra Woodland experiences a Mediterranean climate with a mean annual rainfall of approximately 500 mm (Bureau of Meteorology, Perth). Most rain falls during the cool to cold winter months, although unpredictable summer thunderstorms can occur. The vegetation is dry sclerophyll woodland that includes *Eucalyptus wandoo* on the mid-slopes and *E. accedens*, *E. wandoo*, *E. marginata*, and *Corymbia calophylla* on the upper slopes and plateaux (Coates 1993).

Field experiments

The impact of woylie digging on soil nutrients at the patch scale was examined using simulated digging experiments (Garkaklis *et al.* 2000). Identification of new woylie diggings requires an enormous survey effort. Once an animal has made a number of diggings, the holes remain in the landscape for a considerable period. Therefore, to standardise the time over which the experiment was conducted, simulated diggings with the same characteristics as natural diggings were used. Woylie diggings vary in size, but all have several characteristics in common. As the animal digs downward for a food item, a steep-sided wall is formed to a depth of 10–15 cm, whilst a shallow wall is formed as the soil is ejected to the rear of the animal. Viewed from above, the diggings have a roughly elliptical shape with a spoil heap of excavated soil at one end. In order to examine diggings of known age, holes with the same features as those produced by woylies were dug to a depth of 10 cm (Garkaklis *et al.* 2000). Woylies can make a number of new diggings within a few minutes, and the effects of nutrient input due to animal droppings gathering in the hole (Eldridge and Rath 2002) are unlikely.

Twenty-one pairs of simulated diggings were made in April 1995. From one digging in each pair the soil was collected for nutrient analysis. The other digging in each pair was measured, marked, and allowed to deteriorate with its spoil heap intact for a period of 3 years. In April 1998, soils from the decayed diggings were sampled by carefully excavating each digging to its original dimensions.

Differences in the available soil nutrients over the period of the experiment at the landscape-scale were tested by exclusion of woylie digging. Five 1.5-m-high fences, each enclosing an area of 11 by 11 m, were constructed in June 1994. The central quadrat 10 by 10 m formed the survey area, with the surrounding 0.5 m acting as a buffer to the area disturbed during fence construction and to avoid bias from the droppings of perching birds. All fences were buried to a depth of 0.5 m and the tops of the fences were overhung to deter climbing animals. Three soil samples to a depth of 10 cm were taken at random from each of the 5 exclusion quadrats, at the beginning and end of the simulated digging experiments.

Soil nutrient analyses

All soil samples were placed into sealed polythene bags and kept cool for up to 24 h before transfer to the laboratory for nutrient analysis (Rayment and Higginson 1992). Ammonium and nitrate nitrogen were measured simultaneously using a Lachat Flow Injection Analyser, with ammonium nitrogen concentrations measured colorimetrically at 420 nm using the indo-phenol reaction and nitrite from reduced nitrate measured at 520 nm (Searle 1984). Available phosphorus and potassium were determined by the Colwell method (Rayment and Higginson 1992). Extractable sulfur was measured by inductively coupled plasma spectrophotometry following the techniques outlined in Blair *et al.* (1991). Organic carbon was measured by the method of Walkley and Black and pH measured in 0.01 M CaCl₂ (Rayment and Higginson 1992). Reactive iron was determined spectrophotometrically at 248.3 nm after the soils had been tumbled for 1 h with Tamm's reagent (oxalic acid/ammonium oxalate) employing a soil:solution ratio of 1 : 33 (Rayment and Higginson 1992; Futurefarm, CSBP and Farmers Limited, Perth, WA).

Data analysis

Soil nutrient data were pooled for the initial measurements on the simulated diggings and also for the final measurements, as well as for the initial and final measurements from exclusion quadrats. Inversion of the matrices in the Box M tests for heteroscedasticity in the quadrat nutrient data could not be undertaken. This

situation was encountered in the analysis of repeated measure data from field experiments conducted by Potvin *et al.* (1990). They recommended tests for homogeneity of variance using Bartlett's test applied to the univariate data (Potvin *et al.* 1990). Bartlett's test of the quadrat data showed significant heterogeneity of variance in all variables, apart from available phosphorus (StatSoft 1994). Logarithmic transformation of the data corrected heteroscedasticity. Box M tests for homogeneity of variance (with P set to <0.01) showed no significant heterogeneity of variance between initial and final nutrient measurements in the simulated digging experiment (Potvin *et al.* 1990; StatSoft 1994; Tabachnick and Fidell 1996).

Differences in the initial and final available soil nutrients at the quadrat-scale were tested using multiple analysis of variance (MANOVA) with the single independent variable being the initial and final sample and available soil nutrients were the multiple dependent variables. Differences in the initial and final available soil nutrient contents in simulated diggings were tested using MANOVA with the before and after digging treatment as the single independent variable (Tabachnick and Fidell 1996). Statistical tests were performed using the appropriate modules of STATISTICA (StatSoft 1994).

Results

Patch-scale available nutrients

There was a significant effect of time for available soil nutrients in the decayed diggings (Wilks' lambda = 0.675, d.f. = 7,34, $P = 0.0465$). After 3 years, soil nitrate nitrogen and ammonium nitrogen had significantly decreased ($F = 5.622$, d.f. = 1,40, $P = 0.022$; $F = 4.405$, d.f. = 1,40, $P = 0.042$, respectively) in the decayed simulated diggings (Table 1). Soil sulfur concentrations also decreased significantly in decayed diggings ($F = 5.583$, d.f. = 1,40, $P = 0.023$), but soil phosphorus did not change as a result of digging decay (Table 1; $F = 0.432$, d.f. = 1,40, $P = 0.514$). Changes in soil potassium concentrations approached significance in the decayed simulated diggings (Table 1; $F = 3.731$, d.f. = 1,40, $P = 0.061$, $\beta = 0.49$), and appeared to follow the downward trend of other nutrients, such as nitrate, ammonium and sulfur. There was no change in pH, potassium, iron and organic carbon (Table 1).

Landscape available nutrients

There was no difference in the mean available nutrient levels measured in quadrat samples taken in April 1995 and April 1998 (Wilks' Lambda = 0.841, d.f. = 7,22, $P = 0.755$), all remaining approximately similar after 3 years (Table 1).

Discussion

Soil disturbances in the form of animal burrows and warrens generally result in an increase in soil nutrients, particularly available and total soil nitrogen (Whitford and Kay 1999).

Table 1. Mean (\pm s.e.) values for available soil nutrients in simulated diggings and exclusion quadrats at the start of experiment and 3 years later

Soil parameter	Simulated diggings		Exclusion quadrats	
	Initial value	Final value	Initial value	Final value
Nitrate ($\mu\text{g/g}$)	2.6 \pm 0.3 ^A	1.8 \pm 0.3 ^A	2.5 \pm 0.3	2.5 \pm 0.3
Ammonium ($\mu\text{g/g}$)	5.3 \pm 0.5 ^A	4.1 \pm 0.4 ^A	5.7 \pm 0.5	5.3 \pm 0.4
Sulfur ($\mu\text{g/g}$)	3.8 \pm 0.2 ^A	3.1 \pm 0.2 ^A	3.7 \pm 0.5	3.5 \pm 0.5
Phosphorus ($\mu\text{g/g}$)	3.2 \pm 0.2	3.1 \pm 0.2	2.8 \pm 0.2	3.0 \pm 0.3
Potassium ($\mu\text{g/g}$)	170 \pm 10	146 \pm 8	171 \pm 14	161 \pm 16
Iron ($\mu\text{g/g}$)	650 \pm 50	568 \pm 58	687 \pm 38	655 \pm 36
Organic carbon (%)	2.3 \pm 0.1	2.6 \pm 0.1	3.0 \pm 0.5	2.5 \pm 0.4
pH (CaCl ₂)	6.4 \pm 0.1	6.3 \pm 0.1	6.3 \pm 0.1	6.5 \pm 0.2

^AIndicates a significant difference between the initial and final value.

However, few studies have examined the effects of vertebrates digging for food, rather than constructing burrows, upon the distribution of soil nutrients. Previous studies of woylie diggings have shown that litter accumulates in them as they decay (Garkaklis *et al.* 2000). Litter incorporated into the soil decomposes faster than litter remaining on the soil surface (Stinner *et al.* 1984). Studies of foraging disturbances have found that both the organic matter contents (Steinberger and Whitford 1983; Gutterman 1987) and the rate of organic matter decomposition (Steinberger and Whitford 1983) increase in decayed diggings. This accumulation of organic matter could increase some soil nutrients. For example, almost all terrestrial nitrogen is organically bound and the accumulation of soil nitrogen closely follows the accumulation of soil organic matter (Haynes 1986). An increase in the soil organic matter content of rodent diggings in New Mexico leads to an increase in litter decomposition rates and indicates that total soil nitrogen is increased during this process (Steinberger and Whitford 1983).

No published data could be located reporting the fate of other soil nutrients as a result of the accumulation of organic matter following digging. However, landscape-scale disturbance in the form of storm damage results in an increase in some soil nutrients in *Eucalyptus salmonophloia* woodlands, which grow in slightly lower rainfall zones to the east of our study site. These larger-scale studies have shown that soils under wind-thrown canopies of *E. salmonophloia* have higher concentrations of phosphorus and potassium than undisturbed sites, despite a decrease in organic carbon contents (Yates 1995). Foliar nutrient analysis suggested that storm damage to the woodland canopy disrupts nutrient conservation mechanisms in the trees, so that the leaf litter falling from wind-thrown branches has a higher nutrient level than the litter, composed of senescent leaves, that falls from undisturbed canopies (Yates 1995).

Our study indicated no significant changes in soil nutrients measured at the landscape scale. Rather, there was a decrease in available nitrate, ammonium, and sulfur in the vicinity of the simulated diggings 3 years after the original disturbance. Although no significant decrease in potassium was detected, the high variance in the mean potassium measurements resulted in a low statistical power for this variable. This high degree of variability in potassium values was measured in soils from both quadrats and diggings. Thus, significant decreases in potassium might well be detected if sample replication was increased (Elashoff 1997).

Two factors identified in previous studies of woylie diggings may be implicated in the unexpected decrease in several soil nutrients during this experiment. They are the effects of leaching upon soil nutrients, due to enhanced water infiltration created by woylie diggings in the water repellent landscape, particularly when the diggings are new, and competition for nutrients in a biologically active patch.

Leaching of available plant nutrients

Two soil nutrients examined in this study are susceptible to leaching. They are soil nitrogen, in the form of NO_3^- , and soil sulfur (Russell 1973). In high water infiltration zones, NO_3^- is quickly leached, since anion exchange mechanisms that absorb the nitrate ion in the soil are only weak (Haynes 1986). Therefore, in the preferential water infiltration zone at woylie diggings, there is a high potential for soil nitrate loss, simply due to leaching effects.

Soil nitrogen in the form of ammonium is not susceptible to leaching, since the positively charged ion is readily adsorbed onto negatively charged clay particles (Cameron and Haynes 1986). However, soil ammonium can be quickly nitrified to nitrate (Haynes 1986), particularly after a dry period (White 1979). Without additional ammonium inputs

through the mineralisation of organic nitrogen, the nitrification of ammonium during dry periods should result in a decrease in the overall soil ammonium concentration. Nitrification of ammonium in this way would eventually lead to a decrease in the available nitrogen, because the product of the nitrification process is easily leached from the soil.

Mineralised soil sulfur from organic matter occurs almost entirely as sulfate (Sakadevan *et al.* 1993; Zhao and McGrath 1994). In many soils in Australia, sulfate is adsorbed onto soil colloids and is readily available to plants. However, heavy- and medium-textured soils, with a pH >6, have little capacity to adsorb sulfate. This water-soluble ion is then prone to leaching (Sakadevan *et al.* 1993; Zhao and McGrath 1994). These textural and pH conditions, which occur at the site studied, may be responsible for the decrease in soil sulfur recorded during this experiment.

Despite the decreases recorded in three essential nutrients, no comparable decrease in phosphorus occurred. Phosphorus is not susceptible to leaching (White 1979). Nutrient conservation mechanisms that redeploys nutrients within trees are unlikely to lead to large inputs of phosphorus through a litter made up of senescent *Eucalyptus* leaves (O'Connell *et al.* 1979; O'Connell and Menage 1982), so that little change in the available soil phosphorus content in a decayed woylie digging would be expected.

Competition for mineralised nutrients

High fungal activity among buried organic material has been identified in decayed woylie diggings (Garkaklis *et al.* 2000). Fungi and soil bacteria have a requirement for soil nutrients, particularly ammonium, nitrate, phosphorus, and sulfur (Jennings and Lysek 1996). Although it is possible that there may be an increase in available nutrients early in the decay of woylie diggings, competition between soil fungi, bacteria, and plants may deplete the nutrient supply over time. Available soil phosphorus may decrease very little, since plants can only exploit orthophosphate in the soil solution, whilst soil fungi can scavenge small quantities from the labile pool of phosphorus, and release phosphorus from organic material through the action of phosphatases (Jennings and Lysek 1996). If a slow release of phosphorus occurs as a result of the action of fungi, then available soil phosphorus may remain stable, while other nutrients decrease due to the activity of bacteria and fungi, and also through leaching.

The decline of Australia's digging fauna

These experiments show that digging by Australian vertebrates may affect the spatial distribution of soil nutrients. The digging made by bettongs tends to be clumped together and are most dense within 2 m of trees that host ectomycorrhizae, rather than in the spaces between trees (Johnson 1994). Alterations to the spatial distribution of soil nutrients in woodland soils as a result of digging by bettongs will reflect this pattern. One-third of all recent mammal extinctions have occurred in Australia and many other mammals have experienced significant declines (Burbidge and McKenzie 1989). Many of these extinct and declining species are diggers and burrowers. Consequently, the decline of vertebrate biodiversity over large areas of the Australian continent has implications not only for the conservation of the endemic fauna, but possibly also for ecosystem processes, such as soil heterogeneity, nutrient cycling, and water infiltration.

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