

Does litter decomposition vary between the foraging pits of two soil-disturbing mammal species?

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ABSTRACT: Soil-disturbing animals play a critical role in many ecosystem processes. The loss of native soil-foraging mammals (e.g. greater bilby *Macrotis lagotis*; burrowing bettong, *Bettongia lesueur*) throughout vast areas of Australia has altered fundamental soil processes such as decomposition. Little is known about whether surviving native soil-disturbing animals (e.g. short-beaked echidna, *Tachyglossus aculeatus*) produce soil disturbances that are functionally equivalent to those of locally-extinct native animals. We used a litter bag study to compare abiotic and biotic mechanisms of decomposition within the foraging pits of two native mammal species. We compared decomposition rates between landforms, which we used as a surrogate for soil texture; grass species *Austrostipa scabra* subsp. *scabra* and *Triodia scariosa* subsp. *scariosa*, which we used as our substrates; and the effects of chemically excluding fungi and/or termites. There were initial differences in the organic mass loss between echidna and bilby/bettong foraging pits, with bilby/bettong pits losing more over 30 days, and echidnas losing more over 63 days. However, over 396 days there was no significant difference between the two pit types. Landform (soil texture) and chemical exclusion of termites and fungi did not affect our measures of decomposition until the final stage of the study. The two grass species lost significantly different amounts of organic material at each collection interval, with *Austrostipa* losing more at 30, 63 and 130 days and *Triodia* losing more at the final 396 day collection. This provided the most consistent effect on decomposition. Our results highlight the temporal idiosyncrasies in the various drivers of decomposition in this dune-swale system. Overall, this study provides evidence that the foraging pits of the short-beaked echidna do not differ markedly from those of the locally extinct greater bilby and burrowing bettong in terms of their capacity to maintain rates of decomposition at an annual scale. Copyright © 2015 John Wiley & Sons, Ltd.

KEYWORDS: arid; ecosystem engineer; decomposition; ecosystem function; mallee; woodland

Introduction

In resource-limited ecosystems, soil foraging animals (ecosystem engineers *sensu* Jones *et al.*, 1994) contribute to fundamental ecosystem processes and landscape heterogeneity by creating patches of fertile soil through their foraging activities (Whitford, 2002; Eldridge, 2011). Pits and depressions created by soil-foraging animals capture and retain nitrogen- and carbon-rich sediments, water, litter, faeces and seed, bringing these essential resources together in time and space (Eldridge, 2011). Together, these resources increase microbial and arthropod activity, and should lead to enhanced decomposition (Santos and Whitford, 1983; Whitford, 2002). By controlling the availability of resources to other organisms, foraging pits enable organisms with different resource requirements to co-exist, and can expand the distribution of patch-dependent organisms (Crain and Bertness, 2006).

The decomposition of organic material is a relatively slow yet fundamental process in arid and semi-arid environments (Moorhead and Reynolds, 1991; Throop and Archer, 2008;

Cornwell *et al.*, 2009). Global trends suggest that litter decomposition rates are closely linked to litter chemistry, rainfall and temperature (Cornwell *et al.*, 2008; Brandt *et al.*, 2010). However, decomposition rates in semi-arid and arid environments are generally faster than predicted by these factors alone, with evidence that substrate fragmentation, soil texture, solar exposure and nitrogen availability also play important roles (Austin and Vivanco, 2006; Throop and Archer, 2008). One important factor driving decomposition is burial, with buried organic material decomposing faster than litter residing on the soil surface (Moorhead and Reynolds, 1991; Austin *et al.*, 2009). Burial enhances mineralization and incorporation of nitrogen and carbon into soil organic pools by reducing photodegradation (Austin and Vivanco, 2006; Austin *et al.*, 2009), buffering temperature, prolonging exposure to moist conditions, and bringing decomposing substrate into direct contact with soil-borne fungi and microarthropods. These conditions create an environment conducive to sustaining stable populations of decomposers (Santos and Whitford, 1983; Moorhead and Reynolds, 1993). Therefore, abiotic factors that vary with soil depth are likely more important for decomposition than abiotic

factors that vary only spatially at the surface (Moorhead and Reynolds, 1991; Doblas-Miranda *et al.*, 2009).

Despite the importance of decomposition, relatively few recent studies have focussed on the biotic interactions driving decomposition in arid and semi-arid environments (but see Buitenwerf *et al.*, 2011; Megias *et al.*, 2011). Biotic activity is generally inhibited by the extreme conditions in arid and semi-arid environments. Despite this, suites of soil biota interact to disperse, comminute, digest and mineralize organic material in arid systems, enhancing decomposition. For example, soil arthropods and some vertebrate fauna transport the immobile decomposers such as fungi between decomposition hotspots (Hawkins, 1996; Whitford, 2002). Fungi are important decomposers (Santos and Whitford, 1983; Parker *et al.*, 1984) as they are capable of digesting recalcitrant materials such as cellulose, hemicellulose and lignin (Parker *et al.*, 1984; Hawkins, 1996; Cornwell *et al.*, 2009). Their activity, however, is limited by nitrogen availability, as they tend to immobilize nitrogen during the decay process for use in their digestive enzymes (Parker *et al.*, 1984; Moorhead and Reynolds, 1993). Termites also have an important role in decomposition as they are responsible for both above- and below-ground decomposition (Whitford *et al.*, 1982; Gutierrez and Whitford, 1989). Termites are highly abundant in Australia's arid and semi-arid regions (Whitford *et al.*, 1992; Noble *et al.*, 2009). Australian termites are unique as they tend to be detritivores rather than herbivores, feeding upon 'fungal gardens' of senescent plant material stored in subterranean galleries (Noble *et al.*, 2009). Together, the combination of termites and fungi are presumed to be responsible for substantial amounts of decomposition in Australia's arid and semi-arid environments.

Perhaps of equal or greater importance to decomposition in these environments are the organisms that act relatively independently of seasonal environmental constraints, such as soil-foraging animals (Whitford, 2002). However, during the past 200 years in Australia, many soil-disturbing animals such as the greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*), have had their inhabitable range substantially reduced (Strahan, 1995; Johnson, 2006; Woinarski *et al.*, 2011). Given their important role in small scale patch formation in semi-arid systems (James *et al.*, 2009), the loss of these animals is likely to have widespread effects on soil processes such as decomposition. Little is known about whether surviving and analogous native soil-disturbing animals such as the short-beaked echidna (*Tachyglossus aculeatus*) create disturbances that are functionally equivalent disturbances to the locally-extinct animals. Given that foraging pits dug by short-beaked echidnas differ in size, shape, frequency of construction and location to the foraging pits dug by greater bilbies and burrowing bettong, there may be important differences in the decomposition rate of substrates in these foraging pits.

In this study we assess whether pit morphology (shape) affects the abiotic and biotic drivers of decomposition rates. We compared decomposition rates in relation to a novel suite of factors, specifically, foraging pit shape, landform, substrate type, and detritivore activity. We designed a litter bag study using two pit types of varying in morphology that were either (1) shallow basin-shaped (echidna), or (2) deep, cylindrical-shaped (bilby/bettong). We expected to measure faster decomposition within deeper pits due to the more rapid, deeper burial of litter. The influence of soil texture was assessed by comparing decomposition on a dune (sand) with an inter-dunal swale (loam). We adopted a reciprocal transplant approach using two grass substrates; a dune species (*Triodia scariosa* subsp. *scariosa* N.T. Burb.) and a swale species [*Austrostipa scabra* subsp. *scabra* (Lindl.) S. W. L. Jacobs & J. Everett] and expected greater decomposition of swale substrates in the swales and *vice versa* ('home field advantage'; *sensu* Milcu and Manning, 2011). To assess detritivore effects, we used four treatments involving the use of a termiticide, fungicide, both or none, and

predicted that decomposition would be greatest where neither termiticide nor fungicide was applied to the substrates.

Methods

Study site

This study was undertaken inside Australian Wildlife Conservancy's Scotia Sanctuary in south-western New South Wales, Australia (33°43' S, 143°02' E). This area is semi-arid, receiving approximately 250–280 mm rainfall annually, based on records since 1995. However there are very few years when this amount is actually received due to the spatial and temporal variability of rainfall within and between years. Average daily temperatures range from a minimum of 6°C to a maximum of 17°C in winter (July), and from a minimum of 19°C to a maximum of 33°C in summer [January, Bureau of Meteorology (BOM), 2012]. The soils at our sites are a mixture of brownish and siliceous sands and loamy calcareous earths.

Our study was conducted in two open woodland communities that occur on different landforms: (1) dune mallee woodlands (henceforth Dune) and (2) semi-arid sand plain woodlands (henceforth Swale). The dune mallee woodland occurs on the crests of long, low (relief to 7 m) east–west trending sand dunes. The overstorey is dominated by Eucalypt mallee trees, *Eucalyptus gracilis*, *E. dumosa* and *E. socialis* with an understorey dominated by scattered perennial hummock grasses (*Triodia scariosa*) (Westbrooke *et al.*, 1998). The semi-arid sand plain woodlands tend to occur on soils which have calcareous subsoils. The overstorey is dominated by *Casuarina pauper*. The understorey is predominantly perennial shrubs, including *Alectryon oleifolius* subsp. *canescens*, *Eremophila sturtii*, *Senna artemisioides*, *Acacia burkitti* and *Dodonaea viscosa* subsp. *angustissima*. Ground cover is predominantly *Austrostipa* spp., however ground cover is highly variable and heavily dependent on annual rainfall (Westbrooke *et al.*, 1998).

Foraging pit morphologies

We used the foraging pits of echidnas and greater bilbies (or burrowing bettongs), to compare litter decomposition rates. Echidna pits are generally elliptical shaped, ranging from 15 to 25 cm in diameter, 5 to 15 cm deep (Eldridge and Mensinga, 2007) and are approximately 0.0096 m³ in volume (James and Eldridge, 2007; Eldridge *et al.*, 2012). The pits are typically surrounded by large clods of soil that are ejected during pit excavation. In coarse-textured soils the ejected soil clods are relatively poorly aggregated, with the degree of aggregation increasing in finer textured soils (Eldridge and Mensinga, 2007). Bilbies and burrowing bettongs pits are cylindrical-shaped, approximately 15 cm wide and 10–20 cm deep, on average, 0.0099 m³ in volume (James and Eldridge, 2007) and are largely indistinguishable. In coarse-textured soils, bilby and bettong pits tend to be deeper (James and Eldridge, 2007). The material ejected from these pits is generally piled into a regular mound at the base of the pit.

Litter substrates

For our litter substrates we selected two perennial grasses; *Austrostipa scabra* subsp. *scabra* (henceforth *Austrostipa*) from the swale and *Triodia scariosa* (henceforth *Triodia*) from the dune as our litter substrates. *Austrostipa* is a C3, tufted perennial grass to 0.5 m high with a small surface area to weight ratio. *Austrostipa* is one of the dominant grass species in the swales, but occasionally grows on the dune crests. *Triodia* (porcupine grass), is a C4 perennial hummock grass to 0.6 m high which may form rings

up to 3 m in diameter. *Triodia* has a dense, rigid texture with a high surface area to weight ratio due to the high leaf silica content (Reid and Hill, 2013). *Triodia* is found almost exclusively on the crest of sandy dunes. Both grasses flower in response to rainfall.

Decomposition study

To provide a chemically and physically consistent substrate, living material of *Austrostipa* and *Triodia* was collected from the study site in January 2009. While living material may not be completely chemically equivalent to freshly senesced material, particularly in nitrogen content, the use of senesced material poses issues for capturing the initial stages of decomposition. Grass samples were air-dried at room temperature and stored in the dark for three months before use. Four grams (± 0.5 g) of either *Austrostipa* or *Triodia* were weighed and sealed into aluminium flyscreen bags (12.5 cm \times 12.5 cm; mesh size 2 mm). Substrates were folded down to an appropriate size where necessary to avoid cutting, which exposes excess surface area. An additional set of transport and handling control litter bags were used to adjust our measures of grass mass. Five of each grass and chemical treatment combination ($n = 40$) were taken to and from the field site (1200 km away from our laboratory) to account for litter mass loss through transportation. These bags were handled and transported in exactly the same manner as our sample litter bags. The chemical analyses of the control litter bags formed the baseline data for our decomposition models (i.e. time zero).

Litterbags of both grass species were divided into four treatments, termiticide only (T), fungicide only (F), both termiticide and fungicide (F + T) and no treatment (control, C). All bags were soaked in water for two hours and air dried in the dark for a week prior to treatment to remove any dust or surface residue which may contribute to errors in mass calculations. Treatment solutions were mixed, with 0.05% bifenthrin solution which is used primarily as a termiticide, but can affect bees, flies, cockroaches, mosquitoes, spiders, ants, aphids, leaf-feeding caterpillars, wasps, weevils, leaf miners and leaf hoppers. For our fungicide we used 0.03% triforine solution, which is commonly used to control blackspot, rust and powdery mildew. Litterbags requiring only a termiticide or fungicide treatment were soaked for 12 hours in their respective solution. Litterbags requiring both treatments were soaked in the termiticide solution for six hours, air dried for a week then soaked in the fungicide solution for six hours. Control litterbags were soaked for 12 hours in water. All treated bags were air dried in a dark location for a week. Once dried, all field experiment bags and 'transport and handling' control bags were transported to the field site in plastic zip-lock bags.

Litterbags were placed in four 'blocked' sites. At each site, bags were placed in two landforms: (1) a sandy dune crest and (2) an adjacent swale. In each landform, pairs of foraging pits were located representing one of each morphological shape (echidna and bilby/bettong). Pairs were less than 2 m apart. Litterbags with matching grass type (*Austrostipa*, *Triodia*) and chemical treatment (F + T, F, T, C) were placed into each pair of pits and tethered in the pit with a wire peg. Each pit contained only one litter bag to avoid disturbance with litterbag removal over time. Litterbags were deployed on May 16, 2009. Paired litterbags were collected at one of four time periods, 30, 63, 130 and 396 days since placement (Total $N = 512$). At each collection, litterbags were collected and transported in individual paper bags.

Upon returning to the laboratory, all litterbags were oven-dried immediately at 60°C for 72 hours. The soil and leaves that had accumulated on the outside of the bags were gently removed and discarded. Bags were visually inspected for the presence of fungal spores and termite damage before and after oven drying. Once dried, the entire contents of each litter bag was removed

and weighed. Two subsamples (0.5–1 g) from each litter bag were ashed at 550°C for six hours, cooled overnight in a dessicator and weighed to assess the mass of inorganic matter. This process removes all organic material in the subsample and allows an average calculation of the organic and inorganic content for each litter bag (Throop and Archer, 2008). This process was also used on the 'transport and handling' controls to calculate initial organic and inorganic contents for each grass type and each chemical treatment. We used these controls to calculate the proportion of organic and inorganic content remaining for each sample (as a percentage of the initial material).

Relative success of fungicide and termiticide

We assessed the relative success of our fungicide and termiticide treatments with a two-way permutational analysis of variance (PERMANOVA). We used a binary presence/absence to measure the presence of fungi, termite, and 'other' soil biota activity in the litter bags. Data were transformed using a Bray Curtis resemblance matrix with a dummy variable. Our predictors included treatment (F, T, F + T, C) as a fixed factor and collection interval as a random factor. We ran each of the three response variables (fungi, termite, other) in a separate PERMANOVA using 9999 permutations with Type III error in the +PERMANOVA package for PRIMER (Anderson *et al.*, 2008).

Measures of decomposition

We used two measures of decomposition: (1) percentage of initial organic material remaining, and (2) the rainfall adjusted mass of material lost (in g mm^{-1}). To standardize for the effects of rainfall on mass loss, the grams of material lost were divided by the millimetres of rainfall which had fallen on the study site during the entire deployment of each bag. Rainfall data (total for the duration of each collection interval) were collected at the study site.

To determine how our factors influenced our measures of decomposition, we ran several split plot, five-factor, analysis of variance (ANOVA). Our design compared the effects of Block (random), Landform (fixed), Grass type (fixed), Chemical treatment (fixed) and Pit shape (fixed), and their interactions. Each collection interval (Times 1–4) was analysed separately to simplify the model. Data were tested for homogeneity of variance using Levene's test prior to analysis and no transformations were required. These analyses were performed in the Minitab version 17 statistical software (Minitab 17 Statistical Software, 2010). Fisher's least significant difference (LSD) test ($\alpha = 0.05$) was performed as our *post hoc* test on all significant results.

Modelling decomposition rates

To model the relationship between the percentage litter mass remaining and time (days), we fitted a negative exponential decomposition model to all replicates (Olson, 1963):

$$\ln(X_n/X_0) = -kt$$

where X_0 is the initial amount of material, X_n is the amount of material at time n , and t is the measure of time in days (Olson, 1963). Linear regressions were used to calculate decay rates (k -values), where the coefficients of determination (R^2) express the variance explained by the model. To calculate the half-life of litter (i.e. the time required for 50% decomposition) from our models we used Olson's (1963) formula:

$$t_{0.5} = 0.6931/k$$

To assess the effects of our factors on the decomposition rates and half-lives of our litter, we used the five-factor, split plot ANOVA described earlier. The k values were multiplied by 1000 prior to analysis.

Results

Relative success of fungicide and termiticide

As our following analyses depend upon the assumption that our chemical tests were effective at deterring specific biota we first need to test the relative success of our chemical treatments. This 'success' depends on two factors: (1) the incidence of 'attempted detritivory' by our target organism and (2) the relative effectiveness of the treatment at inhibiting the target organisms. Fewer fungal spores were evident on the litter bags treated with fungicide (Pseudo- $F_{3,496} = 12.7$, $P = 0.002$; Figure 1). The incidence of fungal activity varied over time, with fewer litter bags showing evidence of fungal activity in the final collection (Pseudo- $F_{3,496} = 3.8$, $P = 0.009$). The reduction in apparent shifts in fungal activity made the relative success of our fungicide vary over time (Pseudo- $F_{9,496} = 2.2$, $P = 0.020$; Figure 1).

There were no differences in the incidence of termite activity among treatments ($P = 0.06$) or collection intervals ($P = 0.51$) and few litter bags showed evidence of termite activity. However, the fungicide and termiticide were effective at reducing activity of other detritivores such as insect larvae. The litter bags collected at the final collection interval (396 days) were the only bags showing evidence of non-target detritivore activity (i.e. 'other', such as moth and beetle larvae; collection intervals: Pseudo- $F_{3,496} = 229.3$, $P < 0.001$). From these, all chemically treated litter bags reduced the incidence of breakdown by non-target organisms compared with the control (chemical treatment by collection interval interaction: Pseudo- $F_{9,496} = 5.5$, $P < 0.001$).

Organic mass loss

There was a significant effect of grass species on decomposition rate ($P < 0.02$ for all time periods; Figure 2; Supporting Information Table S1). *Austrostipa* lost more organic material than *Triodia* for the first three collection intervals, but by the end of the study *Triodia* had less percentage organic material remaining than

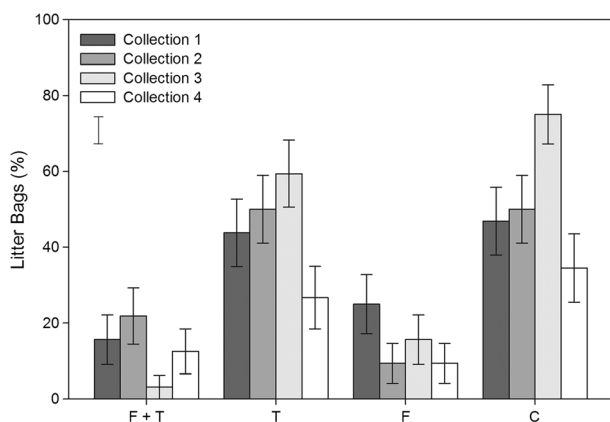


Figure 1. The mean (\pm standard error) incidence of fungal presence for each chemical treatment over the four collection intervals. The bar indicates the 5% least significant difference (LSD) for the Treatment by Time interaction. The incidence of fungal presence is given by the percentage of litter bags with fungi spores present for each factor. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

Austrostipa (Figure 2). We found that the significance of our remaining factors, and their interactions, varied over time.

Initially, there were significant differences in the percentage organic material remaining between our two pit types. After 30 days there was less organic material remaining in the bilby/bettong pits than the echidna pits ($F_{1,48} = 9.31$; $P < 0.01$; Table S1), but after 63 days, significantly less organic material remained in the echidna pits ($F_{1,48} = 8.28$; $P < 0.01$; Figure 2). By the third and final collection intervals, there were no differences in organic material remaining between pit types ($P > 0.3$; Table S1).

For the chemical treatments, there was no significant difference in the organic material remaining until the final collection interval ($P > 0.09$). At the final collection interval more organic material remained for the chemically treated (F, T, F + T) than the untreated ($F_{3,42} = 4.38$; $P = 0.011$; Table S1; Figure 3) litter bags. Differences in percentage organic material remaining between the two grass types at the completion of the study was more pronounced in the swale, with *Triodia* generally losing more organic material than *Austrostipa* (three-way interaction: $F_{3,42} = 3.28$; $P = 0.033$; Figure 3, Table S1).

Litter mass loss adjusted for rainfall

The loss of organic material was still significantly different among our factors when we accounted for the effects of rainfall (Figure 2). However, the results were time-dependent. *Austrostipa* lost a significantly greater mass of organic material per millimetre of rainfall than *Triodia* over the first three collection intervals ($F_{1,42} \geq 6.99$; $P < 0.02$; Supporting Information Table S2). More organic material was lost, per millimetre of rainfall, in echidna than bilby/bettong pits up to 63 days ($F_{1,48} = 5.13$; $P < 0.028$; Table S2) but the pit effect then diminished ($P \geq 0.11$). Rainfall-adjusted mass varied significantly with treatment only after 396 days, with termiticide-treated bags (T and F + T) retaining significantly more organic material per millimetre of rainfall than bags subjected to fungicide only or no chemical treatment ($F_{3,42} = 3.12$; $P = 0.039$; Table S2).

Modelling decomposition rates

The exponential decomposition models fitted our empirical data well (R^2 range = 0.41–0.98; Supporting Information Table S3). The k -values from our modelled decay rates (percentage organic remaining per day) did not differ significantly among any of the treatments or their interactions ($P > 0.07$; Supporting Information Table S4). The modelled half-life of our litter did not differ significantly in relation to our chemical treatments ($P > 0.10$; Table S4) except for control litter bags in the Swales, which had a greater half-life than those under any other chemical or landform combinations (Treatment \times Landform interaction: $F_{3, 42} = 2.88$; $P = 0.049$; Figure 4; Table S4).

Discussion

This study examined whether mechanisms underlying the decomposition of leaf litter differed between the foraging pits of native soil-foraging mammals. Although initial differences in decomposition were detected between echidna and bilby/bettong pits, by the end of the study (396 days) there was no difference in modelled decomposition rates between the two pit types. The most consistent difference was between the two grass species. There was no consistent evidence that landform or chemical exclusion of decomposers (i.e. termites and fungi) significantly reduces the percentage organic material loss, despite significant effects at the final stages of our study.

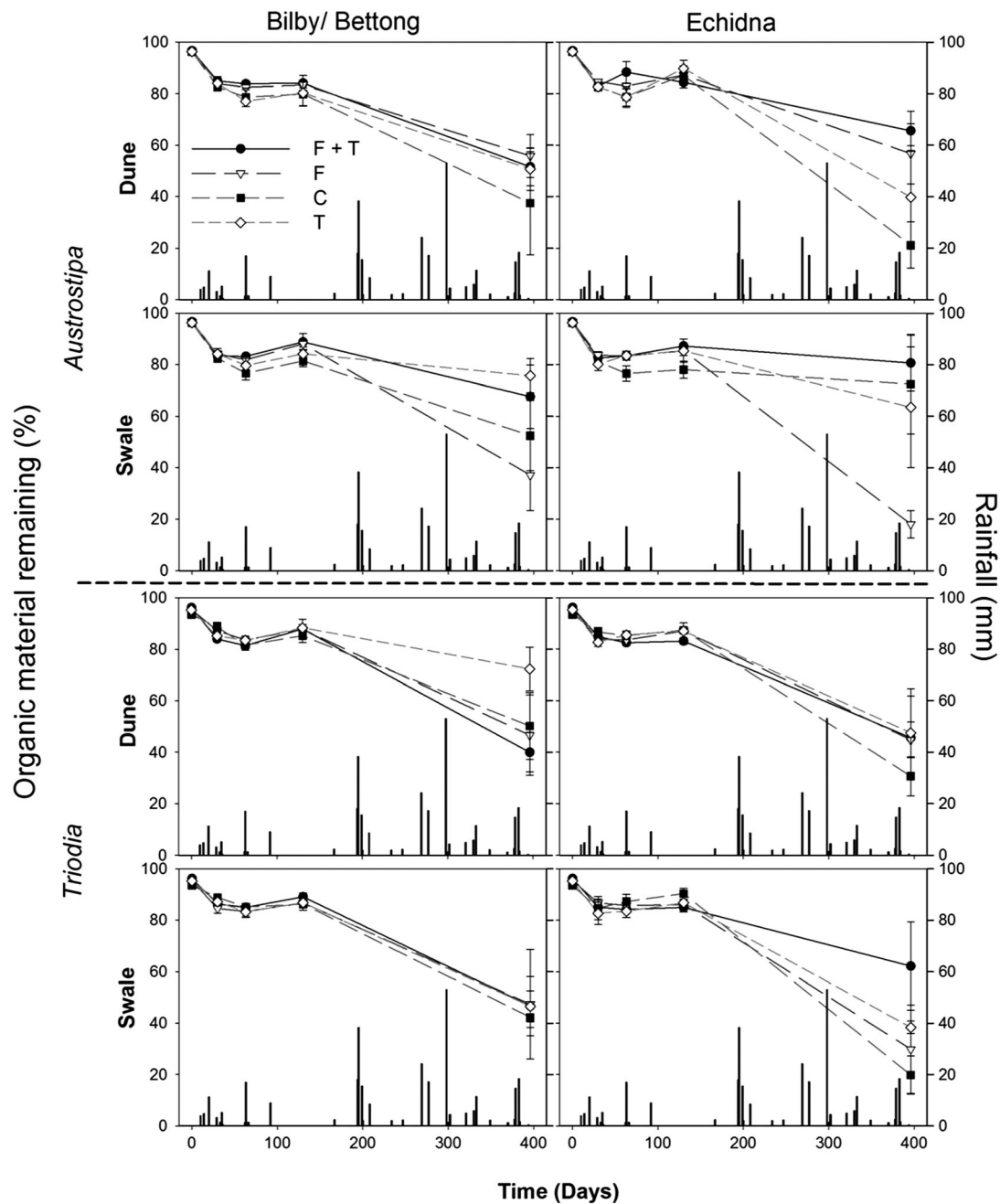


Figure 2. The mean (\pm standard error) percentage organic material remaining over time for each factor, and total daily rainfall (in millimetres) during the study period. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

Effects of foraging pit morphology

The loss of soil-foraging mammals from large parts of arid and semi-arid Australia could potentially alter carbon and nutrient dynamics in these systems. Arid and semi-arid Australia still supports some soil-foraging animals such as goannas (*Varanus* sp., Whitford, 1998), echidnas (Eldridge and Mensinga, 2007) and European rabbits (*Oryctolagus cuniculus*, James *et al.*, 2011), their foraging pits are morphologically distinct, and are constructed at different locations and frequencies to those constructed by locally extinct bilbies and bettongs (James *et al.*, 2009; Eldridge *et al.*, 2012). Although echidnas, bilbies and bettongs all produce similar size excavations, they differ in shape and the depth to which they dig (James and Eldridge, 2007).

Foraging pit morphology initially affected organic mass loss, but the trends were unexpected. Our expectation of greater decomposition in bilby/bettong pits was upheld initially. We

found a greater percentage organic mass loss in bilby/bettong pits after 30 days. This may have been due to a greater initial infiltration of soil into the litter bags in the bilby/bettong pits, particularly in coarse-textured dune soils. However, when organic mass loss was adjusted for the possible effects of rainfall, the initial loss of organic material was greater in the echidna pits. The organic mass loss was also significantly greater in the echidna foraging pits after 63 days. Our results suggest that variation in depth and shape between echidna and bilby/bettong pits has a negligible effect on the long-term process of decomposition. Although the initial burial and rates of organic mass loss may vary between these two uniquely different morphologies, the differences were short-lived, lasting for only a few months. This suggests that, unlike rabbits (James *et al.*, 2011), the foraging pits of short-beaked echidnas have similar functional roles to the foraging pits from the locally extinct bilbies and burrowing bettongs.

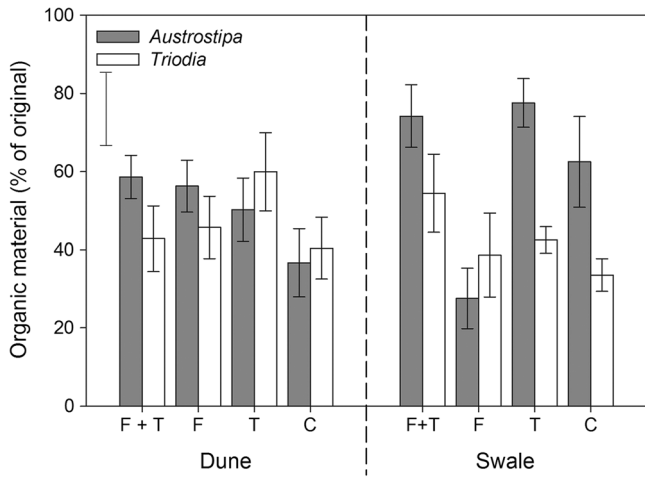


Figure 3. Three-way interaction of Grass type, Landform and Treatment at collection interval 4 (396 days) for the remaining percentage organic material. The least significant difference (LSD) at 5% is given for the three-way interaction. F+T=both fungicide and termiticide, T=termiticide, F=fungicide, C=control.

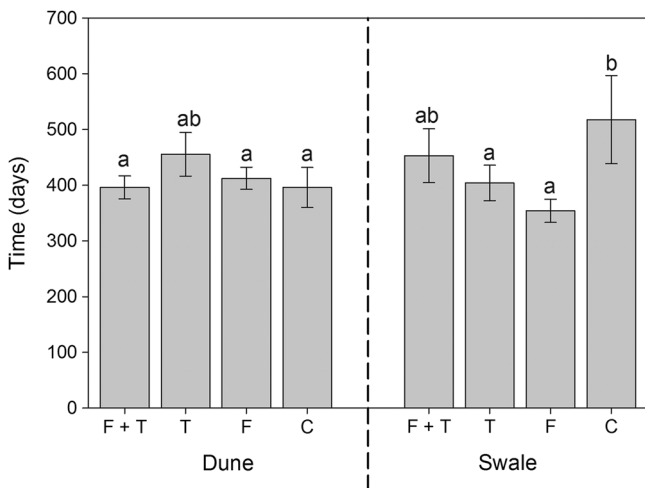


Figure 4. Modelled half-life (\pm standard error) for our Landform by Treatment interaction. The time of the half-life is indicated in days (y axis). F+T=both fungicide and termiticide, T=termiticide, F=fungicide, C=control.

The importance of substrate and soil

Foraging pits enhance decomposition by promoting the rapid burial of organic material (Whitford, 2002). Rates of decay can shift with changes in abiotic conditions such as season and climate (Moorhead and Reynolds, 1991; Austin *et al.*, 2009). However, there is mounting evidence to suggest that the physical and chemical properties of the decomposing substrate are significant drivers of decomposition rates (Cornwell *et al.*, 2008). At global scales, the potential for litter to decompose is consistently correlated with the ecological strategy of individual species making up that litter, given that plant functional traits tend to overlap substantially in their leaf traits (Wright *et al.*, 2004; Cornwell *et al.*, 2008). We found that the two different substrates provided the most consistent effect on decomposition, with significant differences between the substrates at almost every collection. While both of these perennial grasses have a thin cylindrical structure, they do differ markedly in their leaf density due to the high silica content in *Triodia* (Dengler *et al.*, 1994; Reid and Hill, 2013). Such differences in

density affect the surface area to weight ratio, which may affect mass loss rates, because equal masses, rather than equal volumes of each grass were used in each litter bag. Some studies have shown that leaves with a high mass per unit area have low rates of decomposition (Wright *et al.*, 2004; Cornwell *et al.*, 2008).

Our results suggest that soil texture affects the rates of substrate burial and initial decomposition. Soil texture also has a significant effect on foraging pit longevity (Eldridge *et al.*, 2012), with lower half-lives of pits formed on coarse-textured than fine-textured soils (Eldridge, 2011). We used landform as a surrogate for soil texture, comparing decomposition rates from sandy dune crests with loamy inter-dunal swales. While we found no direct effects of our two landforms on decomposition, soil texture appeared to mediate other interactions. For example, the modelled half-life of litter was greatest for litter bags placed in the swale with no chemical treatment. This observation is consistent with predictions under the inverse texture hypothesis (*sensu* Noy Meir, 1973), where coarse-textured sandy soils are more productive than finer-textured soils in low rainfall (< 300–500 mm) environments due to the hydrodynamics of evaporation (Noy Meir, 1973). Not all landform interactions, however, were consistent with the inverse texture hypothesis. For example, at the completion of the study there was more mass loss for the fungicide-treated *Austrostipa* litter bags in the Swales than in the Dunes.

We found no evidence to support a 'home-field advantage' (*sensu* Milcu and Manning, 2011; Fraser and Hockin, 2013) of decomposition for our substrates in the landforms from which they were derived. At the end of the study both untreated grasses had lost equal proportions of organic material in the Dunes, and *Triodia* had lost a significantly greater proportion in the Swale than the locally native *Austrostipa*. This supports previous studies which have also failed to find evidence that plants encourage soil biota which decompose their litter quicker (e.g. Ayres *et al.*, 2006).

The effect of decomposer exclusion

Contrary to expectation, we found that fungi and/or termites were not important decomposers in our system (*sensu* Noble *et al.*, 2009). We expected that excluding detritivores would reduce both proportional and rainfall-adjusted organic mass loss, but this only occurred at the final collection interval. Furthermore, the chemical treatments did not clearly reveal the extent to which fungi or termites decomposed the material. While there was a significantly higher incidence of fungi on the litter bags which were not treated with fungicide (i.e. termiticide and control bags), fungi were temporally variable, peaking at the second and third collection intervals (63 and 196 days). This may have been due to seasonal variation and the timing of our collections, which coincided with warmer weather (63 and 196 days). These periods may have coincided with condition when the physical and chemical state of our substrate is optimal for fungal proliferation.

In arid and semi-arid systems, soil biotic activity is concentrated in the top few centimetres of the soil, corresponding with the zone of maximum nutrients (Whitford, 2002) and disturbance by soil-foraging animals (James *et al.*, 2009; Eldridge *et al.*, 2012). There are conflicting views about whether soil disturbance by animals disrupts or encourages the activities of soil biota such as termites (Gibb, 2012). We found little evidence, overall, of termite activity in our litter bags, which is interesting given that termites are recognized as important decomposers in these systems (Noble *et al.*, 2009). At sites supporting high populations of both termites and beetles, termites tend to be more important consumers, particularly of lignin-rich material (Cornwell *et al.*, 2009). Our results, however, indicate that insect larvae, which likely include beetles

and moths, may be as equally as important for the decomposition of sub-surface material as termites, and this might be the case elsewhere in semi-arid Australia (Hart, 1995).

The litter bags collected at the final interval were heavily consumed by non-target insect larvae, particularly in the non-treated bags. Even treated bags still showed evidence of insect larval attack. Given the large rainfall events that occurred during the summer (between 196 and 396 days), insect larvae may have been unusually common and therefore played a greater role in the decomposition process than has been previously recorded. Detritivory by similar insect larvae has been recorded in decomposition studies conducted during years of above-average rainfall in eucalypt-pine woodlands in eastern Australia (Hart, 1995).

Concluding Remarks

In this study we examined the relative effect of ecosystem engineering by two vertebrates and a range of invertebrates on the decomposition of litter across a Dune–Swale ecosystem. Difference in pit type was not a major driver of decomposition. Rather, decomposition processes were more complex, with marked temporal effects, largely driven by seasonal conditions (rainfall) rather than the identity of the decomposer organisms. Overall, shallow echidna pits were equally as effective as deep, bilby pits, suggesting that echidnas provide a functionally equivalent ecosystem engineering role to the locally extinct native animals such as the bilbies, at least in our study environment. However, our study tells us nothing about likely effects of engineering by non-native species such as the European rabbit (*Oryctolagus cuniculus*) that also digs pits. Overall this study provides evidence that the foraging pits of echidnas do not differ markedly from those of the locally extinct bilby/bettong, at least in terms of their capacity to maintain decomposition. Despite this, a diverse community which contains an array of resource patch-creating species is likely more functional than one where species have been lost. We found no clear soil texture (landform) effect on decomposition apart from some idiosyncratic effects of various substrates. Our results should therefore be applicable to systems dominated by sand dunes and associated fine-textured soils.

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