

Landform and vegetation patch type moderate the effects of grazing-induced disturbance on carbon and nitrogen pools in a semi-arid woodland

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Abstract

Background and aims Dryland soil organic carbon (C) pools account for a large portion of soil C globally, but their response to livestock grazing has been difficult to generalize. We hypothesized that some difficulty generalizing was due to spatial heterogeneity in dryland systems. We examined the importance of heterogeneity at vegetation and landform scales on the response of litter and soil C and nitrogen (N) to grazing.

Methods Litter and soil C and N pools were quantified in different vegetation microsites (tree, shrub, open) and landform elements (dune, swale) across a grazing disturbance gradient in an eastern Australia semi-arid woodland.

Results Vegetation, landform, and grazing disturbance affected litter and soil C and N pools singly and through interactions. Resource pools were distributed unevenly across vegetation and landforms, and were largest beneath trees in swales. Grazing reduced pools

in vegetation-landform combinations where pools were greatest. Pool increases from high to moderate disturbance sites were minimal.

Conclusions Litter and soil C and N pools are strongly affected by livestock grazing, although responses to grazing relaxation may be non-linear. Accurately predicting C and N responses to grazing in drylands will require accounting for patch differences at multiple spatial scales.

Keywords Litter · Nutrient pools · Patch heterogeneity · Soil organic carbon · Spatial scale

Abbreviations

SOC	Soil organic carbon
C	Carbon
N	Nitrogen
[SOC]	SOC concentration
[N]	Soil nitrogen concentration
SOC _{area}	SOC mass per area in g m ⁻²
N _{area}	Soil N mass per area in g m ⁻²
litter _{area}	Litter mass per area in g m ⁻²

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Introduction

Drylands (arid and semi-arid ecosystems) play a crucial role in the global carbon (C) cycle, accounting for more than 10 % of terrestrial biomass C and up to 30 % of soil organic carbon (SOC) globally (Scurlock

and Hall 1998). Although C pools are typically low in drylands relative to more mesic environments, dryland soils account for a large amount of SOC because of their extensive global distribution (circa 40 % of the earth's terrestrial surface; Derner and Schuman 2007). Even small changes in SOC dynamics in drylands can therefore have potentially large effects on global C cycling and storage. Given the importance of SOC as a sink or source for atmospheric C, land management practices that affect SOC dynamics may play an important role in affecting the balance between SOC uptake and loss. Understanding and predicting soil C pools and dynamics in drylands are critical for global C accounting. However, doing so remains challenging in these systems, in part due to the lack of understanding of the roles of spatial heterogeneity, land management, and land use history (Houghton et al. 1999).

Grazing-induced disturbance by domestic livestock causes substantial degradation in drylands globally (reviewed in Asner and Archer 2010) through a variety of direct and indirect processes. Trampling by livestock typically increases soil bulk density and compaction, exposes surface soil aggregates to wind and water erosion, and destroys biotic crusts that are important for soil stability and SOC pools (Bowker et al. 2011; Eldridge et al. 2011). Ultimately, trampling reduces soil surface structure, negatively affecting processes such as infiltration and erosion, and eventually modifying long-term productivity. More indirectly, grazing alters plant cover and diversity (Midgley et al. 2010), potentially changing the quality of inputs into the soil by increasing the relative contribution of grazing-tolerant plant species at the expense of species preferred by grazers (e.g., palatable plants or non-woody plants; Diaz et al. 2007). Grazing also generally reduces the quantity of inputs to surface litter pools (McKeon et al. 2009). The quantity and quality of above- and belowground litter inputs may in turn affect SOC pools and stability (Witt et al. 2011). Furthermore, a reduced litter layer alters soil microclimate (Golodets and Boeken 2006) via effects on surface evaporation, soil moisture and infiltration, and, therefore, negative feedbacks on litter decomposition processes (Bromham et al. 1999). Given the slow recovery of soils in dryland systems, areas with a long history of heavy grazing are likely to exhibit strong legacy effects on soil C and nutrient cycling processes (Eldridge et al. 2011). While gross changes in SOC pools have been studied widely, few studies have

addressed how grazing affects the distribution of these pools across different microsites that are typical of spatially heterogeneous dryland systems.

Grazing disturbances may vary spatially at multiple scales as grazers can be highly selective and drylands exhibit inherent spatial heterogeneity. Grazing effects on ecosystem processes are therefore unlikely to be uniform through space. Drylands tend to be structured into two distinct patch types; one that is a net source of resources and another that is a net sink (fertile patches or 'fertile islands' *sensu* Garcia-Moya and McKell 1970). Resource accumulating areas typically form beneath shrub or tree canopies and have higher levels of water, litter, nutrients, and sediment and therefore higher biological activity, productivity, and diversity than more sparsely vegetated or bare intercanopy areas. This patchiness in vegetation and soils exists at a range of spatial scales, where differences in the intensity of fertile island effects are a function of shrub age/size, often exhibiting strong within-patch spatial patterns (Throop and Archer 2008). Grazing has the potential to enhance the fertile island effect if animals redistribute resources from interspaces to shrub islands or to enhance the competitive ability of woody species (Scholes and Archer 1997). Furthermore, larger-scale patterns of heterogeneity may be superimposed on fertile/infertile patches, affecting both the relative distribution of nutrients in fertile/infertile patches and the patterns by which grazing influences redistribution between these patch types.

The semi-arid woodlands of eastern Australia are characterized by a patchy distribution of perennial woody plants (trees and shrubs) located within a less productive matrix of herbaceous vegetation, often with sparse levels of cover. Across this region, fertile islands are nested within two major landforms: dunes and swales. Sandy soils predominate on the dunes, which support a moderately dense cover of relatively short woody eucalypts (mallees) with a sparse understory of scattered *Triodia* grass hummocks and little other vegetation. In contrast to dunes, loamy soils in swales support a variable, and generally extensive, cover of shrubs (*Dodonaea* spp., *Senna* spp.), grasses (*Austrostipa* spp., *Austrodanthonia* spp.), tall trees (*Casuarina pauper*), forbs, and cryptogamic crusts. Processes of runoff and erosion from the dunes to the swales reinforce the general increases in resource capture and retention in the swales. Native fossorial mammals were historically important drivers of soil

processes in these systems (James et al. 2009), although predation by non-native cats and foxes has reduced their abundance in many areas (Morton 1990). Intensive livestock grazing in this region occurs primarily from sheep and feral goats.

We examined differences in surface litter, soil C, and soil nitrogen (N) pools within dunes and swales in a semi-arid eastern Australian woodland. We predicted that these two landscape elements would vary in nutrient capture and retention, and hence that pools would differ dramatically. Within each landscape element, we examined the differences in pools among three different vegetation patch types (trees, shrubs, open interspaces) across a gradient representing increasing levels of grazing-induced disturbance and decreasing importance of native fossorial mammals. Based on the heterogeneous structure of these ecosystems we developed four hypotheses about the factors affecting the spatial patterns of litter and soil C and N pools in relation to the disturbance gradient: 1) increasing disturbance by grazing would result in declines in the relative sizes of soil and litter pools, 2) absolute pool sizes would be greater in the swales than on the dunes due to the greater clay content, and therefore increased capacity to retain soil organic matter, and additions of run-on, resulting in greater plant productivity in the swales; 3) pool sizes under tree and shrub canopies would be greater than those in the open interspaces, consistent with expectations under the fertile island phenomenon, and 4) declines in soil and litter pools with increasing grazing disturbance would be consistent among landforms and vegetation patches (Fig. 1). We examined pool size differences in order to determine whether differences in soil C and N pools across a grazing-induced disturbance gradient are moderated by different landforms and vegetation patches.

Materials and methods

The research was conducted in a semi-arid woodland area in western New South Wales, Australia (33°24' S, 141°21' E). Mean annual precipitation of about 250 mm is highly variable. Mean annual temperature is 25.5 °C, with mean maximum and minimum temperatures of 31.9 °C and 19.1 °C, respectively. We worked in three adjoining sites with contrasting management histories and with varying degrees of

contemporary grazing-induced disturbance (low, moderate, and high): a conservation reserve, a research station, and a commercial pastoral property (Table 1). The low disturbance site was a fenced area within the Australian Wildlife Conservancy's Scotia Sanctuary where domestic livestock grazing has historically been low due to a lack of surface water. All domestic (goats, sheep) and feral (cats, foxes, goats, rabbits) animals were removed at this site and low densities of native animals (burrowing bettong, *Bettongia lesueur*; greater bilby, *Macrotis lagotis*; nailtail wallaby, *Onychogalea fraenata*) were reintroduced in spring 2008. The reserve also included a low density of western grey (*Macropus fuliginosus*) and red (*Macropus rufus*) kangaroos. The moderate disturbance site was a paddock at the University of Ballarat's Nanya Research Institute. The paddock was originally lightly grazed until the 1930s, and then grazed at rates comparable to pastoral properties until 1995 when domestic grazing animals were removed. It still, however, contained feral livestock and native herbivores. The high disturbance site was in an area of extensive pastoral leasehold paddocks where domestic livestock grazing has historically been moderate to high, typical of most grazing properties in the semi-arid woodlands of eastern Australia.

Field sampling

Within each of the three grazing disturbance sites, we collected soil and litter samples from seven areas, each comprising two adjacent landforms: a dune and interdunal swale. The dunes are west–east trending, approximately 200 m wide, and separated by interdunal swales, about 500 m wide. Dunes were dominated by deep, sandy soils and supported a community of mallee eucalypts (*Eucalyptus oleosa*, *E. socialis*), a widespread vegetation type that tends to accumulate extensive pools of surface litter around the base of the trees (Bradstock 1990). The dunes also supported a discontinuous layer of *Triodia scariosa*, a hummock-forming grass characterized by lignin-rich waxy leaves that form vertical spikes. *Triodia* is a grass, but for the purpose of our study we treated it as a shrub as it is exceptionally long-lived and is the dominant mid-story component of these systems. *Triodia* grows in a ring-like pattern with individual clumps of plants up to 5 m across. The adjacent low-lying swales are characterized by soils with loamy to clay loam surface textures, and function as run-on zones, receiving water

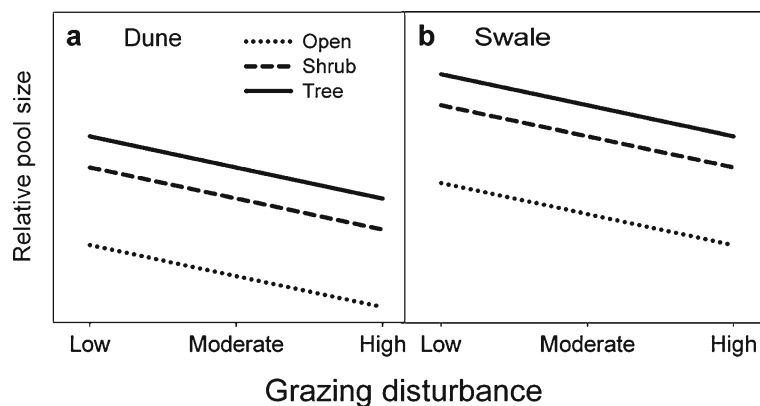


Fig. 1 Hypothesized changes in litter and soil carbon (C) and nitrogen (N) pools in response to grazing-induced disturbance. We hypothesized that resource pools would 1) decline in response to greater grazing disturbance, 2) be greater in the more productive and clay-dominated swales than in dunes, and,

and sediment from the dunes. The swales are dominated by *belah* (*Casuarina pauper*) trees and variable densities of the shrubs *Eremophila sturtii*, *Dodonaea viscosa* and *Senna* spp. Small herbaceous vegetation often grows beneath tree canopies and in open inter-canopy areas in swales.

Within each landform pair, we collected samples from three different vegetation microsites: open (unvegetated soil surface), shrub (*Triodia* in the dunes or *Eremophila/Dodonaea* in the swales), and tree (mallee in the dunes or *belah* in the swales). Microsites were blocked, such that the three microsites (tree, shrub, open) were always sampled in close proximity (<15 m apart) to each other. Shrub and open locations

consistent with the fertile island phenomenon, 3) be greater beneath shrubs and trees than in open areas. We also expected that 4) resource pools would decline similarly across vegetation microsites and landforms in response to grazing disturbance

were at least one tree canopy width away from the closest neighboring tree. In total, we had 378 litter/soil sampling locations (3 sites along the disturbance gradient \times 2 landform elements \times 7 landform pairs \times 3 microsites \times 3 microsite blocks).

For each of the three microsite blocks in each landform site, samples were collected from a different cardinal direction relative to the focal vegetation (E, NW, or SW). For shrubs, samples were taken close to the base of *Triodia* plants (dunes) or in the mid-canopy (swales). Although mid-canopy samples from all shrubs would have been ideal, *Triodia* forms dense tussocks, making it impossible to sample underneath the plant. For trees, samples were

Table 1 The historical and current abundance and type of grazing animals at the three grazing disturbance sites. The abundance of each species was converted into dry sheep equivalents (DSE). Calculations of DSE based on current DSE-equivalent values for a range of animals: bilby and bettong (0.01), naitail wallaby (0.10), European rabbit (0.125), red

and grey kangaroo (30–40 kg; 0.625), sheep and goats (1.0). Data were obtained from records of bilby, bettong and naitail wallaby data from Australian Wildlife Conservancy, unpublished estimates of rabbit, kangaroo and goat numbers for western New South Wales (NSW) and long-term average sheep stocking rate figures from western NSW

Current grazing disturbance	Domestic livestock grazing history	Current grazing rate (DSE)	Types and densities of grazers present (km ⁻²)	Area (km ²)
Low	Ungrazed until 1930. Low levels of grazing from 1930 to 1990 due to lack of surface water	0.70	bilbies, bettongs, naitail wallabies (10–42), grey and red kangaroos (<0.1)	37
Moderate	Ungrazed by domestic livestock until 1930, then moderate to high levels up until 1999, when grazing by domestic livestock ceased; feral goats remain	1.97	kangaroos (0.3), rabbits (1500), goats (30)	40
High	Moderate to high levels of domestic livestock from 1850 to the present	3.84	kangaroos (0.3), rabbits (1500), goats (40), sheep and cattle (100)	75

collected mid-way between the trunk and the canopy edge. Litter was collected from within a 21 cm diameter quadrat placed on the soil surface. Volumetric soil cores were collected to 5 cm deep with a 4.7 cm diameter cylindrical corer. Because SOC and N pools are most dynamic in surface soils, grazing-induced spatial patterns are likely to be easily detectable at this depth (Derner et al. 1997; McClaran et al. 2008). Different changes with greater soil depths, however, are also possible.

Laboratory analyses

Litter and soil samples were air dried in the field, oven dried at 60 °C in the laboratory until no further mass loss occurred, and weighed. Litter was separated into four categories: leaf, woody (bark and twigs < 1 cm in diameter), dung, and other (other varied among sites, but was primarily plant reproductive material and litter fragments too small to identify as leaf, woody or dung material). Litter mass for each category at all sampling locations was recorded. Litter was then pooled for each category by vegetation microsite by landform element by grazing disturbance combination ($n=72$). A subsample of the pooled litter was ground with a Cyclone Mill (UDY Corporation, Fort Collins, CO) and analyzed for C and N concentration ([C] and [N]) on an elemental analyzer (ECS 4010; Costech Analytical, Valencia, CA).

Dried soils were passed through a 2 mm sieve to remove any coarse fragments and weighed. A subsample of each sieved soils was cleaned for visible litter fragments and pulverized in a ball mill (8000D; SPEX, Metuchen, NJ). Soils were acid fumigated to remove any carbonates present (Harris et al. 2001) and analyzed in triplicate for C and N content on an elemental analyzer. Bulk density was calculated as the mass of the fine earth (< 2 mm) fraction divided by the volume of the entire core, thus accounting for volume displaced by > 2 mm fragments (Throop et al. 2012). Bulk density was used to convert SOC concentration ([SOC]) and soil [N] to mass per unit area (SOC_{area} and N_{area} ; g m^{-2}). Soil labile carbon concentration was determined using a simplified laboratory method whereby slightly alkaline, dilute KMnO_4 reacts with the readily oxidisable (active) carbon, converting Mn (VII) to Mn(II), and lowering the absorbance of 550 nm light (Weil et al. 2003).

Statistical analysis

We examined differences in response variables in relation to three levels of disturbance, two landforms and three microsites using mixed-model ANOVAs with three error terms. The first stratum considered disturbance level, the second stratum landform and its interaction with disturbance, and the third stratum microsite and its two- and three-way interactions with disturbance and landform. Data were checked for homogeneity of variance (Levene's test) and normality using diagnostic tests and transformed (primarily \log_{10}) where appropriate. For all analyses, significant differences between means were examined using Fisher's Protected Least Significant Difference (LSD) test where the effect was significant. We used permutation multi-variate ANOVA (PERMANOVA; Anderson et al. 2008) to examine differences in the composition of litter (i.e. sticks, leaves, dung, other) in relation to disturbance, landform and microsite using the same structure as above. The matrix of litter composition was converted to a similarity matrix using the Bray Curtis similarity coefficients contained within the PRIMER-E statistical package. Pair-wise *a posteriori* comparisons were made, where necessary, using a multi-variate analogue of the *t* statistic, the probability levels being obtained by permutations. Thus it was unnecessary to correct for a large number of multiple comparisons.

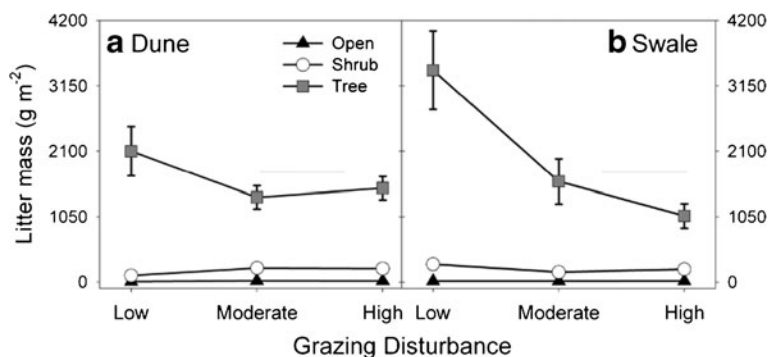
Results

Litter pools

Litter mass per area ($\text{litter}_{\text{area}}$) was negatively related to grazing disturbance under trees, but was insensitive to grazing under shrubs and in open areas (Fig. 2; Disturbance x Microsite: $F_{4,240}=4.30$, $P=0.002$; Appendix). However, $\text{litter}_{\text{area}}$ response to disturbance differed among landforms (Disturbance x Landform: $F_{2,18}=11.77$, $P=0.001$). Across vegetation microsites, $\text{litter}_{\text{area}}$ was least in open areas and greatest beneath trees ($F_{2,240}=416.97$, $P<0.001$).

There were substantial differences in litter composition between the low and the two higher grazing disturbance sites (Pseudo $F_{2,18}=2.68$, P (perm)=0.004; Appendix). This was driven by a greater proportion of the 'other' category and a lower proportion of dung at the low disturbance site (Table 2). There

Fig. 2 Litter mass (g m^{-2}) in sites across a grazing disturbance gradient in **a**) dunes and **b**) swales in open area, shrub and tree microsites. Litter mass is the total of litter from four categories (leaf, woody, other, dung). Values presented are means \pm standard error



was a significant effect of landform on litter composition, with proportionally more leaf litter and less 'other' material in the swales than on the dunes (Pseudo $F_{1,18}=5.65$, P (perm)=0.001). This landform effect was most pronounced in the high grazing disturbance site (Disturbance \times Landform: Pseudo $F_{2,18}=1.99$, P (perm)=0.028). Litter composition differed among vegetation microsites, with open microsite litter dominated by woody material, shrub microsite litter dominated by leaf material, and tree microsite litter more evenly distributed among leaf, woody, and 'other' categories (Pseudo $F_{2,240}=100.82$, P (perm)=0.001;). Additionally, there was proportionally less dung on dunes in open areas than in all other landform-vegetation microsite combinations (Landform \times Microsite: Pseudo $F_{2,240}=4.19$, P (perm)=0.001).

Table 2 The mass (g m^{-2}) of litter made up of leaf, woody, other, and dung material across a grazing disturbance gradient, and subdivided into vegetation microsites (open, shrub, tree) within the three grazing disturbance sites. Litter values for

Disturbance and microsite	Leaf	Woody	Other	Dung
Low	358 \pm 73.5	316 \pm 49.4	304 \pm 77.2	3 \pm 1.5
Open	4 \pm 0.8	7 \pm 2.0	1 \pm 0.6	0 \pm 0.1
Shrub	119 \pm 27.6	67 \pm 19.8	8 \pm 2.7	5 \pm 4.1
Tree	957 \pm 190.3	879 \pm 103.6	909 \pm 205.0	4 \pm 1.9
Moderate	201 \pm 44.7	193 \pm 27.1	161 \pm 33.3	11 \pm 3.0
Open	4 \pm 0.9	13 \pm 4.8	1 \pm 0.5	1 \pm 0.5
Shrub	113 \pm 23.7	53 \pm 9.4	23 \pm 5.8	4 \pm 1.5
Tree	486 \pm 120.9	511 \pm 53.8	459 \pm 82.9	30 \pm 8.1
High	189 \pm 32.6	163 \pm 23.3	126 \pm 26.7	26 \pm 7.0
Open	3 \pm 0.5	9 \pm 2.2	2 \pm 0.5	5 \pm 2.0
Shrub	110 \pm 22.7	55 \pm 9.8	27 \pm 8.3	19 \pm 6.9
Tree	455 \pm 80.5	425 \pm 48.1	350 \pm 68.0	56 \pm 19.1

Leaf litter [C] and [N] were similar across both the grazing disturbance gradient (42.56 ± 0.01 %C, 1.12 ± 0.005 % N; Appendix) and vegetation microsites (42.57 ± 0.02 % C, 1.12 ± 0.004 % N). Between landforms, leaf [C] remained similar (42.60 ± 0.02 % C), but there was significantly greater tissue [N] for leaf litter from plants growing in the swales (1.29 ± 0.08 % N) than those on the dunes (0.90 ± 0.08 % N; $F_{1,9}=11.54$, $P=0.008$).

Soil pools

Grazing disturbance, landform, and vegetation microsite all strongly influenced soil bulk density. Bulk density was greater in the high disturbance site (1.75 ± 0.02 g m^{-3}) than in the low (1.62 ± 0.02 g m^{-3}) or moderate (1.65 ± 0.02 g m^{-3}) disturbance sites ($F_{2,18}=8.70$,

grazing disturbance are means \pm standard error of all microsite and landform sampling locations within a disturbance site; litter values for microsites are means \pm standard error of both dune and swale landforms within microsite and disturbance categories

$P=0.02$; Appendix). Bulk density was also greater on dunes ($1.73\pm 0.02\text{ gm}^{-3}$) than in swales ($1.62\pm 0.02\text{ gm}^{-3}$; $F_{1,18}=10.96$, $P=0.004$), and in the open ($1.79\pm 0.02\text{ gm}^{-3}$) and under shrubs ($1.76\pm 0.02\text{ gm}^{-3}$) than beneath trees ($1.47\pm 0.02\text{ gm}^{-3}$; $F_{2,240}=113.96$, $P<0.001$).

The concentration of SOC increased with reduced grazing disturbance (Table 3; $F_{2,18}=6.81$, $P=0.006$; Appendix). Among landforms, [SOC] and was greater in swales than on dunes (Fig. 3a-b; $F_{1,18}=8.57$, $P=0.009$) and tended to be greater in low disturbance swales than in any other grazing disturbance-landform combination. Across microsites, [SOC] decreased significantly from beneath trees to under shrubs and in the open ($F_{1,18}=360.69$, $P<0.001$), and this microsite effect was most pronounced on the dunes (Landform x Microsite: $F_{2,240}=9.12$, $P<0.001$). In the swales [SOC] was greatest under trees and shrubs in low grazing disturbance (Disturbance x Landform x Microsite: $F_{4,240}=3.40$, $P=0.01$), but on the dunes microsite differences across the grazing gradient were not significant. The response of SOC_{area} to grazing disturbance varied among landforms and microsites. In the swales, SOC_{area} was elevated under trees and shrubs in low grazing disturbance, but there were no clear patterns in dunes (Fig. 3c-d). Between landforms, SOC_{area} varied in different ways among the three vegetation microsites. SOC_{area} beneath trees was greater on

dunes (920 gC m^{-2}) than in swales (829 gC m^{-2}), but generally greater on swales than dunes under shrubs and in the open (Landform x Microsite: $F_{2,240}=10.43$, $P<0.001$). SOC_{area} increased across vegetation microsites, being least in open areas and greatest beneath trees ($F_{2,240}=243.64$, $P<0.001$).

On average, concentrations of soil labile C increased with reduced grazing disturbance (Fig. 3e-f; $F_{2,18}=50.21$, $P<0.001$; Appendix). Between landforms, swales had substantially greater labile C concentrations than dunes at the low disturbance site, but the differences were much smaller in moderate to high disturbance sites (Disturbance x Landform: $F_{2,18}=9.88$, $P=0.001$). Similarly, the decline in labile C from tree to open microsites was much greater under low (370 mg C kg^{-1} difference), than moderate to high grazing disturbance (Table 3; $170\text{--}320\text{ mg C kg}^{-1}$ difference; Disturbance x Microsite: $F_{4,240}=7.95$, $P<0.001$).

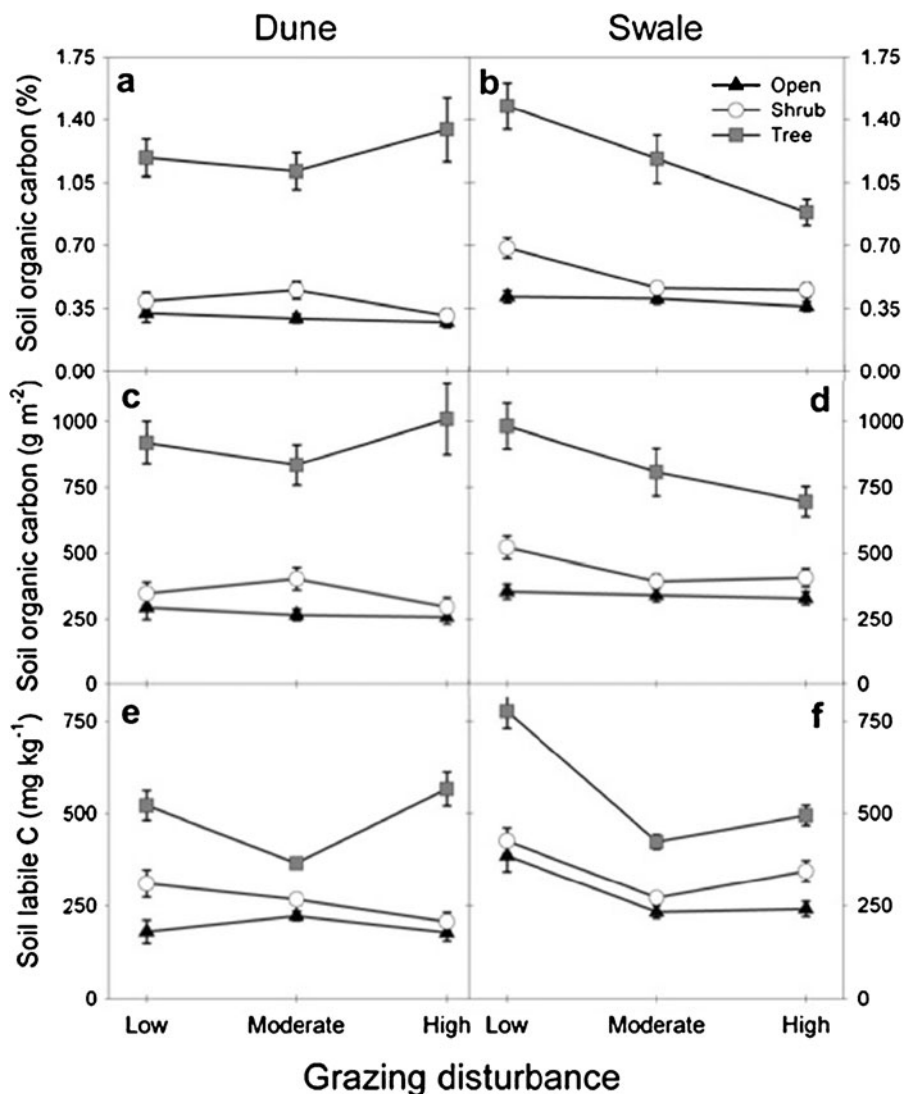
Like [SOC], soil [N] was greater in swales than on dunes (Fig. 4a-b; $F_{1,18}=54.53$, $P<0.001$; Appendix), and was greater in low disturbance swales than in any other grazing disturbance-landform combination (Disturbance x Landform: $F_{2,18}=4.05$, $P=0.035$). Across microsites, soil [N] decreased significantly from beneath trees to under shrubs and in the open ($F_{1,18}=350.69$, $P<0.001$). In the swales soil [N] was greatest

Table 3 The percent soil organic carbon ([SOC]), SOC content per area (SOC_{area}), labile soil C concentration (Labile C), percent soil nitrogen (Soil [N]), soil N content per area (Soil N_{area}), and soil C to N ratio (C:N) in sites across a grazing disturbance gradient, and subdivided into vegetation microsites (open, shrub, tree) within the three grazing disturbance sites. Values

for grazing disturbances are means \pm standard error of all microsite and landform sampling locations within a disturbance site; values for microsites are means \pm standard error of both dune and swale landforms within microsite and disturbance categories. Values within a column with the same superscript letters are not significantly different

Disturbance and microsite	[SOC] (%)	SOC _{area} (g C m ⁻²)	Labile C (mg C kg ⁻¹)	Soil [N] (%)	Soil N _{area} (g N m ⁻²)	C:N
Low	0.75 \pm 0.050 ^a	570.9 \pm 34.19 ^a	433.3 \pm 17.6 ^a	0.058 \pm 0.0040 ^a	44.06 \pm 2.597 ^a	13.33 \pm 0.300 ^a
Open	0.37 \pm 0.030	325.1 \pm 26.81	282.4 \pm 30.9	0.032 \pm 0.0027	27.79 \pm 2.304	12.35 \pm 0.422
Shrub	0.54 \pm 0.049	436.0 \pm 32.23	368.2 \pm 26.5	0.044 \pm 0.0042	35.33 \pm 3.107	13.09 \pm 0.503
Tree	1.33 \pm 0.085	951.5 \pm 58.45	649.4 \pm 31.3	0.098 \pm 0.0076	69.04 \pm 4.817	14.56 \pm 0.575
Moderate	0.65 \pm 0.043 ^{ab}	508.6 \pm 29.73 ^a	296.9 \pm 8.8 ^c	0.049 \pm 0.0031 ^a	38.32 \pm 2.036 ^a	13.13 \pm 0.235 ^a
Open	0.35 \pm 0.021	304.6 \pm 17.38	227.3 \pm 10.4	0.029 \pm 0.0018	25.04 \pm 1.521	12.42 \pm 0.349
Shrub	0.46 \pm 0.029	399.7 \pm 25.32	269.1 \pm 9.4	0.037 \pm 0.0019	31.08 \pm 1.632	12.93 \pm 0.432
Tree	1.15 \pm 0.083	821.6 \pm 58.73	394.3 \pm 11.8	0.083 \pm 0.0061	58.84 \pm 4.133	14.04 \pm 0.402
High	0.60 \pm 0.048 ^b	500.3 \pm 35.39 ^a	338.1 \pm 22.8 ^b	0.049 \pm 0.0029 ^a	40.84 \pm 2.160 ^a	11.76 \pm 0.248 ^b
Open	0.32 \pm 0.021	294.6 \pm 19.37	208.9 \pm 15.9	0.030 \pm 0.0020	27.39 \pm 1.834	10.99 \pm 0.320
Shrub	0.38 \pm 0.029	353.1 \pm 26.14	275.2 \pm 21.7	0.035 \pm 0.0026	32.75 \pm 2.338	10.91 \pm 0.298
Tree	1.12 \pm 0.102	852.9 \pm 76.19	530.3 \pm 28.6	0.081 \pm 0.0053	62.37 \pm 4.066	13.37 \pm 0.524

Fig. 3 Soil organic carbon (a, b) concentration (%) and (c, d) per unit area (g C m^{-2}), and (e, f) labile C concentration (mg C kg^{-1} soil), across a grazing disturbance gradient, in dunes (a,c,e) and swales (b,d,f), and in open area, shrub, and tree microsites. Values presented are means \pm standard error



under trees and shrubs in low grazing disturbance (Disturbance \times Landform \times Microsite: $F_{4,240}=3.99$, $P<0.01$), but on the dunes microsite differences across the grazing gradient were not significant. Soil N_{area} response to grazing disturbance varied among landforms and microsites. Across microsites, N_{area} was greater under trees than under shrubs or in open areas, although the relative differences among microsites differed with landform (Fig. 4c-d; Landform \times Microsite: $F_{2,240}=7.64$, $P=0.001$). Like SOC_{area} , N_{area} increased across vegetation microsites, being least in open areas and greatest beneath trees ($F_{2,240}=238.80$, $P<0.001$).

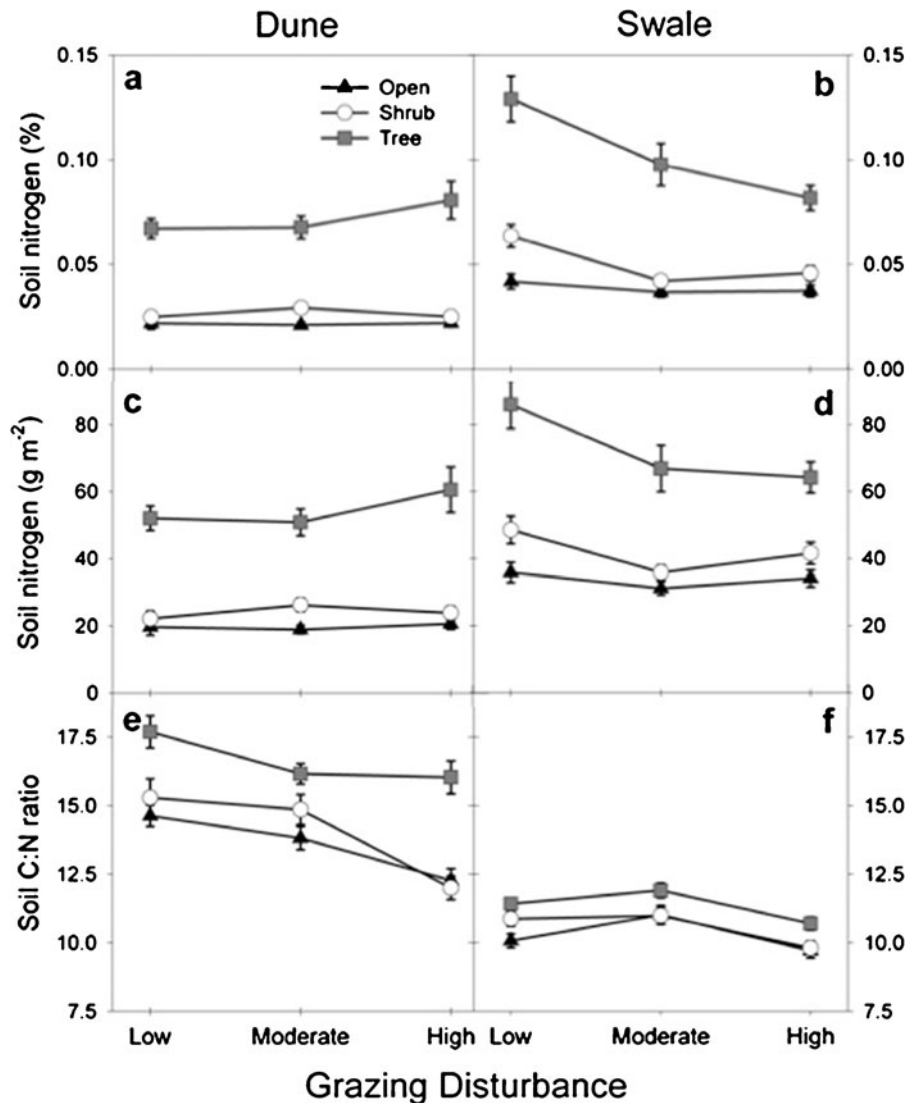
The soil C:N ratio was significantly lower in the high grazing disturbance site than in the moderate

and low disturbance sites ($F_{2,18}=15.72$, $P<0.001$; Appendix), and significantly greater on dunes than in swales (Fig. 4e-f; $F_{1,18}=242.95$, $P<0.001$). The soil C:N ratio was greater beneath trees than under shrubs or in open areas, but the difference was more pronounced on dunes than in swales (Landform \times Microsite: $F_{2,240}=7.02$, $P=0.001$).

Discussion

Over the past few decades there has been considerable interest, yet little consensus, in understanding the role of grazing as a driver of soil nutrient pools (reviewed

Fig. 4 Soil nitrogen (a, b) concentration (%) and (c, d) per unit area (g N m^{-2}), and (e, f) soil C:N ratio, across a grazing disturbance gradient, in dunes (a,c,e) and swales (b,d,f), and in open area, shrub and tree microsites. Values presented are means \pm standard error



in Piñeiro et al. 2010). The results of our study, from the semi-arid woodlands of eastern Australia, indicate that vegetation microsite, landscape position, grazing management, and their interactions, can have marked effects on surface litter, and soil C and N pools. Three important results arose from our study. First, litter and soil C and N pools exhibited variable responses to increasing grazing-induced disturbance; grazing reduced resource pools beneath trees, and somewhat under shrubs, in swales, but pools in dunes and open microsites were unaffected. Additionally, differences between moderate and high grazing disturbance sites were only minor. Second, litter and soil C and N were not distributed evenly across the landscape. Rather,

pools were larger in swales than on dunes, consistent with our hypothesis. This effect, however, was moderated strongly by grazing, whereby greater pools in the swales under minimal disturbance tended to collapse under moderate to high levels of grazing-induced disturbance. Third, pools tended to be highly patchy at small spatial scales associated with different microsites, with larger litter and soil pools under trees than under shrubs or in the open. Overall, our results suggest that predicting changes in soil C and N in drylands will require an understanding of the distribution of different vegetation and landform patch types and the interactions between these and disturbance. Reliable estimates of landscape-wide resource pools

will therefore require rigorous, across-landscape sampling and careful characterization of spatial heterogeneity to guard against extrapolating from a small number of samples (*sensu* Bird et al. 2002).

Grazing effects on litter and soil pools

In our study, the mass per area of surface litter declined markedly with increasing levels of disturbance, particularly in the swales. Grazing-induced disturbance has long been implicated in habitat degradation and substantial reductions in plant diversity and abundance (FAO 2007). It also tends to cause changes in the structure of herbaceous (Schuman et al. 1999) or woody (Archer et al. 1995) plant communities, with subsequent effects on both the quality and quantity of nutrients released into the soil organic pool. Our sampling design focused on vegetation patches and prevented us from explicitly capturing changes in plant community composition that would be expected to alter litter inputs. However, our litter data indicate a shift in composition, with a decrease in leaf and “other” (primarily plant reproductive parts and litter fragments too small to identify) litter from relatively undisturbed to highly disturbed sites, particularly in the swales. A concomitant increase in dung with disturbance, and therefore an increase in proportional transformation of leaf material into dung, potentially influences both the quality and spatial distribution of litter inputs. Apart from direct effects on nutrient inputs, grazing also alters inputs of organic matter by increasing soil bulk density and compaction, and reducing cryptogamic soil crust cover, thereby altering water infiltration processes and increasing trampling-induced erosion (Andrew and Lange 1986; Eldridge et al. 2011).

Soil C and N responses to grazing indicate a combination of shifting inputs and changes in soil physical properties. Declines in soil labile C concentrations with increasing disturbance suggest a reduction in soluble products of decomposing plant cells such as carbohydrates, sugars and lipids (Loginow et al. 1987), either via reduced inputs or more rapid decomposition. The trend in labile C is consistent with the data for [SOC] and [N], which also declined with increasing disturbance. However, although soil C and N concentrations decreased, differences in SOC_{area}

and N_{area} across the grazing gradient were offset by changes in soil bulk density. Bulk density increased with greater grazing disturbance, likely a result of compaction from stock trampling. This apparent lack of change in SOC pools is a commonly reported phenomenon (e.g., Golluscio et al. 2009) and represents a fundamental problem when quantifying the impacts of anthropogenic disturbance on SOC pools (Lee et al. 2009; VandenBygaart and Angers 2006), particularly in soils with poorly differentiated or deep horizons where reporting pools based on genetic horizons is not possible. This problem is magnified at shallow soil depths most affected by compaction; the losses in SOC and labile C concentrations suggest that total pools would decrease with grazing, if greater depths were taken into account.

While reductions in litter and [SOC] were expected under high levels of disturbance, it was surprising that they were equally depressed under moderate disturbance. Current pools likely reflect both contemporary litter deposition processes and past disturbance history, and there is likely to be a strong legacy effect on litter pools resulting from previous management practices. For example, heavy grazing and prolonged drought in the late 1890s is thought to have led to an increase in the cover and extent of monospecific stands of native shrubs such as *Dodonaea viscosa* and *Eremophila sturtii*. Current levels of unrestricted grazing, particularly by feral goats and exacerbated by European rabbits, likely induce shifts in species composition (Tiver and Andrew 1997). Pools of SOC may in turn respond to the compositional responses of grazer diet selection, even when grazing pressure is the same as native grazers (Bagchi and Ritchie 2010). Our study sites reflect a wide range of historical grazing disturbances, and although the moderate grazing site experienced sustained heavy grazing by domestic animals for about 60 years, it ceased only two decades ago (Table 2). Plant production, and subsequent litter production, may remain low following relaxation of grazing (Eldridge et al. 2011) or grazing-induced erosional processes may be causing greater redistribution of litter (Field et al. 2011; Golluscio et al. 2009). Likewise, studies from long-term exclosures in the semi-arid mulga (*Acacia aneura*) woodlands north of our study sites found that the greatest increases in SOC following sheep

destocking occurring after 44 years (Witt et al. 2011), suggesting that our moderate removal site may not yet be in equilibrium from the management shift.

Depressed [SOC] and litter pools in the moderate relative to high grazing sites may indicate a state change resulting from legacy effects of historical grazing, the loss of native, soil-disturbing animals, or a combination of both. Changes in plant species composition, the cover of bare soil, or the relative cover of woody to non-woody plants represent structural shifts in woodland ecosystems that can have positive feedbacks on reduced functions (Briske et al. 2006). Shifts among alternate stable states are common, but reversion to the original state simply by removing the original trigger responsible for change may not be possible (Suding et al. 2004). Indeed, the degradation-restoration framework of (King and Hobbs 2006) predicts that prolonged disturbances, such as increased livestock grazing, will lead to substantial reductions in abiotically-driven functions such mineralization rates, water infiltration or primary productivity. Reversion to the original state may only be possible by injection of considerable energy.

In conjunction with low livestock grazing, soil-foraging animals have been reintroduced to the site at the low end of the gradient. Small, semi-fossorial mammals were a significant component of the biota of the semi-arid woodlands until shortly after European settlement (Morton 1990), and are believed to be critical for the maintenance of soil and ecological processes (e.g., Eldridge et al. 2011). Their foraging pits have been shown to have multiple positive effects on ecosystem processes as broad as enhanced mineralization of

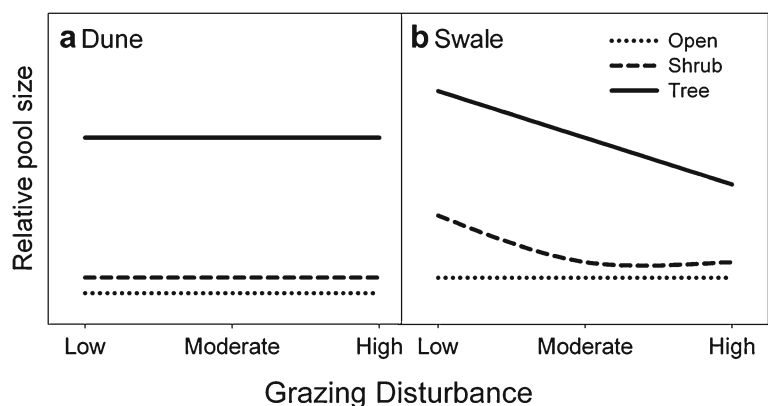
organic matter, greater soil moisture, increased seed germination and richness of microarthropods (Eldridge and Mensinga 2007; James et al. 2010). Nutrient-rich ‘hot spots’ forming in the pits are likely to produce substantial flow-on effects to vegetation and biota of woodland ecosystems. We attribute greater litter pools, labile C, and reduced soil bulk density under low levels of disturbance to the combined effects of native soil-disturbing animals and removal of feral (e.g., European rabbits) and domestic grazing animals. However, we cannot separate out the role of grazing relaxation from the reintroduction of native species.

Landform effects on litter and soil pools

Overall, our results suggest that swales are the resource-rich landforms at the landscape scale. In comparison with dunes, swales had more litter at the least disturbed site, a greater proportion of leaf litter, and greater soil C and N pools. These responses are probably due to the greater clay content in swale soils (25–40 % clay) compared with dunes (<10 % clay; Walker 1991), which would also account for the greater productivity, evident by the larger litter pools and higher litter leaf N.

While landform alone had clear effects on litter and soil pools, the non-linear influence of grazing across landforms was inconsistent with our fourth hypothesis (Fig. 1). We observed the expected linear response of C and N pools in the swales, but pools in dunes were insensitive to grazing disturbance (see revised conceptual model, Fig. 5). This suggests that dunes are more resistant to the effects of grazing-induced disturbance; there

Fig. 5 Revised conceptual model expressing the overarching patterns present across multiple response variables. Model does not include all significant interactions



are several possible reasons for this pattern. First, dune soils have low levels of structural stability and have inherently high bulk densities, which are unlikely to increase with grazing. On the contrary, swale soils are more likely to compact under trampling and hence lead to increases in SOC_{area}. Second, cryptogamic crusts are important components of swale soils (up to 60 % cover) compared with dunes (<5 % cover). Crusts are susceptible to removal by overgrazing and trampling; cryptogams increase soil aggregation and enhance soil nutrients by accumulating C and N with marked effects on ecosystem functions (Bowker et al. 2010). Nitrogen-fixing plants such as *Casuarina pauper* and *Acacia* spp. are also common in swale soils. Thus, biological activity is likely to be lower on the dune soils than in the swales. Given these differences, productivity is likely greater in the swales and therefore grazing activity would be concentrated in the swales, leading to swales being more responsive to grazing disturbance. Finally movement of resource-rich sediments from the dunes to the swales by processes of aeolian and fluvial deposition would reinforce existing higher levels of resources in the swales.

Patch type effects on litter and soil pools

Our data are consistent with the notion of resource concentration around patches of perennial vegetation (fertile islands *sensu* Abanda et al. 2011; Gonzalez-Polo and Austin 2009), where soil and litter pools were substantially elevated around woody plants relative to the open patches. Pools under shrubs, however, were more similar to those in the open than under the trees. We believe that differences in the canopy area of trees and shrubs could explain, in a large part, the differences we observed. The larger size of canopies of both *belah* and eucalypt trees (~ 300 m²) compared with *Senna* and *Eremophila* shrubs (1–2 m², Soliveres et al. 2011) reinforces our view that both above- and belowground inputs would be greater from trees. Woody plant size is often positively correlated with changes in SOC (e.g., Throop and Archer 2008), apparently a function of greater annual inputs and/or a longer duration of inputs. Differences in fertile islands between shrubs and trees may also reflect the relative ability of the

canopy area to retain litter transported by wind or water (Derner et al. 1997), or facilitate herbaceous vegetation (Soliveres et al. 2011).

In contrast to our expectations, pool declines with grazing disturbance were inconsistent among microsites and there were interactions among microsites and landform elements. The strongest sensitivity to grazing disturbance occurred in tree patches in the swales, while open areas remained largely unchanged. The strong response to grazing under trees in swales was likely due to the high subcanopy herbaceous production and shade, which would encourage livestock grazing and camping (Soliveres et al. 2011). High livestock presence in tree patches in swales is supported by the highest dung concentration in this patch type x landform combination. In contrast, litter and soil pools on dunes were largely unaffected by grazing in all three patch types.

Conclusions

Drylands support the majority of the world's livestock and grazing is a substantial disturbance in many of these ecosystems (Asner et al. 2004). Our study shows that in a semi-arid eastern Australian woodland, grazing-induced disturbances alter C and N pools, but the magnitude of these effects are strongly a function of landform and microsite. Due to the vast global extent of drylands, even small changes in dryland C cycling may affect global C pools and dynamics. This study suggests that taking spatial heterogeneity into account will be crucial for accurately predicting and accounting for C changes in response to dryland management.

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Appendix

Significant effects on litter and soil C and N of grazing disturbance (low, moderate, high), landform

(dune, swale), and microsite (open, shrub, tree) factors, and their interactions. *For litter composition F values represent Pseudo F and P values represent P (perm)

Variable	Effect	df	F	P
Litter pool (g m^{-2})	Microsite	2, 240	416.97	<0.001
	Disturbance x Landform	2, 18	11.77	0.001
	Disturbance x Microsite	4, 240	4.30	0.002
*Litter Composition	Disturbance	2, 18	2.68	0.004
	Landform	1, 18	5.65	0.001
	Microsite	2, 240	100.82	0.001
	Disturbance x Landform	2, 18	1.99	0.028
	Landform x Microsite	2, 240	4.19	0.001
	Disturbance x Landform x Microsite	4, 240	1.76	0.012
	Leaf [C]	No significant effects		
Leaf [N]	Landform	1, 18	11.54	0.008
Soil Bulk Density	Disturbance	2, 18	8.70	0.020
	Landform	1, 18	10.96	0.004
	Microsite	2, 240	113.96	<0.001
[SOC]	Disturbance	2, 18	6.81	0.006
	Landform	1, 18	8.57	0.009
	Microsite	2, 240	360.69	<0.001
	Landform x Microsite	2, 240	9.12	<0.001
	Disturbance x Landform x Microsite	4, 240	3.40	0.010
SOC _{area} (g m^{-2})	Landform	1, 18	4.68	0.044
	Microsite	2, 240	243.64	<0.001
	Landform x Microsite	2, 240	10.43	<0.001
Soil Labile C (mg kg^{-1})	Disturbance	2, 18	50.21	<0.001
	Landform	1, 18	26.26	<0.001
	Disturbance x Landform	2, 18	9.88	0.001
	Microsite	2, 240	173.30	<0.001
	Disturbance x Microsite	4, 240	7.95	<0.001
	Disturbance x Landform x Microsite	4, 240	5.49	<0.001
	Soil [N]	Landform	1, 18	54.35
	Disturbance x Landform	2, 18	4.05	0.035
	Microsite	2, 240	350.69	<0.001
	Disturbance x Landform x Microsite	4, 240	3.99	0.004
	Soil N _{area} (g m^{-2})Soil C:N	Landform	1, 18	43.25
	Microsite	2, 240	238.80	<0.001
	Landform x Microsite	2, 240	7.64	0.001
	Disturbance	2, 18	15.72	<0.001
	Landform	1, 18	242.95	<0.001
	Landform x Microsite	2, 240	7.02	0.001

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