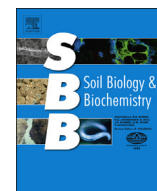




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Complementarity of dung beetle species with different functional behaviours influence dung–soil carbon cycling

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ABSTRACT

Decomposition of large ungulate herbivore dung and its subsequent incorporation into the soil play key roles in carbon and nutrient cycling and are important for grassland productivity. Dung beetles contribute to the initial breakdown and transport of organic matter from the dung into the soil but how they interact with the microbial community to modify decomposition processes remains poorly understood.

Using a mesocosm experiment, we investigated the individual and interactive effect of two dung beetle species with contrasting functional behaviour (dweller species: *Agrilinus ater* (De Geer 1774) vs. tunneller species: *Typhaeus typhoeus* (Linnaeus 1758)) on dung C cycling (CO₂ fluxes and C transfer through the soil profile) and resultant effects on microbial activity and biomass in the soil.

Both dung beetle species contributed significantly to dung removal, reducing the C lost through microbial respiration from the whole mesocosm. However, C concentrations measured in leachates from the mesocosm were only significantly higher in the presence of the tunneller species, indicating that tunnelling activity was required to increase C transfer down the soil profile. The combined effect of the two dung beetle species resulted in the highest soil microbial respiration from the soil and in particular in the 2–10 cm depth increment, suggesting positive complementarity effects between species with different functional behaviour.

We conclude that the return of C in the form of dung in grasslands, coupled with the activity of a functionally diverse dung beetle assemblage, could result in short term fluctuations in soil microbial activity with important consequences for soil C cycling.

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1. Introduction

In grasslands the decomposition of large ungulate herbivore dung and its incorporation into soil play key roles in ecosystem carbon (C) and nutrient cycling. The way in which dung is processed is thus important for the long-term sustainability of the grassland and its productivity (Williams and Haynes, 1995; Zaman et al., 2002; Aarons et al., 2009; Yoshitake et al., 2014). On pasture stocked at rates of 700 cow days ha⁻¹ y⁻¹, dung deposition adds around 22 t ha⁻¹ of C (Bol et al., 2000), providing a significant input of C to soil. This C input is thought to contribute to soil C stocks in temperate grasslands with 10–16% of cow-dung C incorporated

into the soil in only two months (Bol et al., 2000; Dungait et al., 2005). However, a significant proportion of dung–C is lost through microbial respiration (Lovell and Jarvis, 1996; Chen et al., 2011; Grilo et al., 2011). In addition, dung can stimulate microbial activity in the soil underneath the dung, resulting in the loss of pre-existing soil C (Bol et al., 2003). Any factor that modifies microbial decomposition of dung is therefore likely to have a strong influence on the retention of dung- and soil-C in pasture soils. One such factor could be macro-invertebrates, which are responsible for the initial breakdown and transport of organic matter from the dung into the soil (Stevenson and Dindal, 1987; Lee and Wall, 2006).

In many regions a large proportion of dung removal is mediated by dung beetles, which use the dung both for feeding and breeding (Lee and Wall, 2006; Yamada et al., 2007; Nichols et al., 2008). Adult dung beetles feed on the liquid part of fresh dung (Holter, 2000) but some also create tunnels in the soil in which they store dung for further feeding or for the creation of brood balls that host eggs and developing larvae (Cambefort and Hanski, 1991). The activity of

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dung beetles (Owen et al., 2006) and that of other soil macro-invertebrates such as earthworms (Hendriksen, 1997), has been reported to increase the concentration of C in the upper soil horizon. Soil macro-invertebrates, including dung beetles, have also been reported to strongly influence greenhouse gas emissions (e.g. CO₂, N₂O and CH₄) from dung (Lubbers et al., 2013; Penttilä et al., 2013), suggesting that these organisms influence microbial activity and dung decomposition rates. The main mechanisms by which this might occur are: (1) by feeding on dung and increasing the rate at which it dries out on the soil surface, which reduces the amount of resource available for microbes, and (2) by burying dung, which increases its exposure to soil microbes and changes the environment in which it is decomposed. Dung beetle behaviour can also change the surface area of the dung, which alters its accessibility to microbes and may influence the amount of C moved further down the soil profile in leachate.

Although it is clear that dung beetles influence grassland C cycling, we lack any real understanding of how dung beetle species with different functional behaviour and interactions between them affect soil microbial biomass and activity. In temperate grasslands dung beetles are typically subdivided into two main functional types, based on their nesting behaviour: dweller species (adults and larvae feed inside the fresh dung deposits) and tunneller species (adults dig tunnels in the soil under the dung deposit and bury dung for feeding and nesting). Tunneller species have been shown to be much more effective in dung removal than dweller species (Rosenlew and Roslin, 2008; Nervo et al., 2014), but the consequences of this for soil microbial activity and biomass as well as dung C retention in soils remains unknown. Furthermore, whether the two types of species interact to have a non-additive effect on dung decomposition is unknown.

The aim of this study was to examine the individual and interacting effects of two functionally contrasting dung beetle species (a tunneller and a dweller species) on herbivore–dung decomposition, microbial biomass and respiration, and the incorporation of C into the soil. To achieve this we used a mesocosm experimental approach that allowed investigation of interactive effects of two types of dung beetle species under controlled conditions. We test the following hypotheses: (1) dung processing and the transfer of C from the dung through the soil profile will differ in the presence of the two contrasting dung beetle species, being higher when tunneller beetles are present due to their ability to bury large amounts of dung; (2) microbial respiration from dung deposits will be modified by the action of dung beetles, being higher soon after the dung is deposited as dung beetle activity will promote aerobic conditions within the dung, and lower later on as beetle activity accelerates the drying process and depletes the amount of dung resource available for microbes; (3) the interactive effects of the two functionally contrasting dung beetle species on microbial respiration will be synergistic as a consequence of greater physical processing of dung and a potentially larger more active microbial community.

2. Materials and methods

2.1. Experimental design

To examine the effects of dung beetles with contrasting functional behaviour on soil microbial respiration, biomass and dung decomposition rates, we set up a mesocosm experiment at Hazelrigg Field Station in Lancaster (54°00'49.35"N/2°46'30.68"W). Treatments consisted of no dung (Soil only treatment), dung only (Dung treatment), dung plus the dweller species (Dweller species treatment), dung plus tunneller species (Tunneller species treatment), and dung plus both species (Dweller & Tunneller species

treatment). The dweller species was *Agrilinus ater* (De Geer 1774) and the tunneller species was *Typhaeus typhoeus* (Linnaeus 1758). These two species are common in grazed grasslands in the area and use dung for both adult and larval feeding. We used a complete random block design with five replicates of each treatment.

Experimental mesocosms were constructed from 11 cm diameter sections of plastic pipe and were 25 cm in length to allow the tunnelling species to construct nests underneath the dung. Soil (silt loam of the Brickfield 2 association (Avis and Harrop, 1983), % C = 3.05, %N = 0.26, pH = 6.1) was collected from the field station and sieved to 4 mm. After sieving, the soil was homogenized and the same amount (1350 g) added to each mesocosm. The bottom end of the pipe was covered with fine weave plastic netting material to hold in the soil while allowing water to flow through the mesocosm. Plastic 45 mm garden mesh was formed into a cylinder and inserted into the soil at the top of the mesocosms, extending to approximately 9 cm above the top of the pipe. This acted as a support for a covering of fine weave plastic netting material, with a removable lid. The space created at the top of the pipe allowed the dung balls to sit on the top of the soil and be exposed to natural weather conditions. The fine weave plastic netting allowed the sun and rain to take effect as well as preventing colonization of the dung by flies and other beetles. The lid covers were removed from all mesocosms after 20 days, once it was certain that the dung had ceased to attract other organisms, and to allow the beetles to leave the dung before their food resource had been completely consumed, representing natural behaviour (Koskela, 1972).

A. ater specimens, along with the dung used for the experiment, were collected from a sheep-grazed field on Bailrigg Farm in Lancaster (54°01'08.40"N/2°47'25.98"W). Tunnelling beetles (*T. typhoeus*) were collected from rough cattle grazing fields at Warton Crag Nature Reserve (54°09'07.53"N/2°46'45.49"W). Sheep dung was used for the experiment; it was collected fresh and free of beetles from the field and mixed together in a bucket and then formed into balls of equal size (mean wet weight of 199.79 ± 0.02 g), and frozen for 48 h. Dung was fully defrosted before being added to the appropriate mesocosms. Twenty representative dung balls were also oven dried at 60 °C to obtain a dry weight. Beetles were added to appropriate treatments with numbers of *A. ater* determined through allometric scaling of biomass, such that $B = M^{3/4}$ (where *B* is the metabolic rate and *M* is body mass) (West et al., 1997). This allowed species assemblage numbers to be more representative of those found in the field than through biomass alone and also to standardise biomass across treatments. For treatments containing *A. ater* equal numbers of males and females were added (28 individuals per mesocosm in the single species treatment and 14 individuals in the mixed-species treatment). For treatments containing *T. typhoeus*, only females were included (2 in the single species treatment and 1 in the mixed-species treatment). Mesocosms were sealed with the mesh lids immediately after the beetles were added. The experiment was set up on the 28th May 2010 and allowed to run for 6 weeks in the field to enable both adult and larval dung beetle effects on the dung to be included (Rosenlew and Roslin, 2008).

2.2. Dung removal

At the end of the experiment, dung remaining on the soil surface was removed from the mesocosms and weighed before being dried in an oven at 60 °C and then reweighed. The amount of dung lost during the experiment was assessed in two ways: (a) comparison between the original and final wet mass of each dung ball allowed us to measure the amount of dung lost due to both dung removal by beetle activity and the drying effects of time (Slade et al., 2007; Rosenlew and Roslin, 2008) and (b) the dried weight of fresh

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