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Functionally rich dung beetle assemblages are required to provide multiple ecosystem services

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ABSTRACT

Dung beetles mediate a variety of important ecosystem services in both natural and human-modified habitats. These services are associated with the exploitation of dung by beetles for breeding and feeding, with different functional groups using dung in different ways. While many studies have considered how individual ecosystem functions and services (primarily dung removal and seed dispersal) are affected by changes in dung beetle diversity, fewer studies have considered the consequences for multiple functions and services. We used manipulative experiments to evaluate the functional efficiency of three species of dung beetles, each representing one of the three functional groups present in temperate Europe. Standardising beetle biomass, we compared single-species treatments to a three-species mixture containing each of the species in equal biomass. We then measured three ecosystem services relevant in supporting pasture-based livestock production systems: dung removal, soil fauna activity, and soil aeration. The presence of dung beetles significantly elevated all three ecosystem services. However, delivery of each service peaked under different treatments, indicating that no single-species assemblage can provide maximum functioning across multiple services. For all three services, the three-species polyculture provided a level of functioning indistinguishable from the most efficient single-species treatment. Our results highlight the importance of considering multiple functions and services when assessing the relationship between biodiversity and ecosystem functioning, and suggest that the conservation of functional richness within dung beetle communities could play an important role in securing the delivery of multiple ecosystem services.

1. Introduction

Rapid changes in land use, driven largely by the intensification of agriculture over the past century, have resulted in widespread declines in species associated with agricultural landscapes (Butler et al., 2007). Many of these species help maintain agricultural productivity by providing ecosystem services: biological, physical, and geochemical processes occurring within an ecosystem that benefit humankind (De Groot et al., 2002). These services may become diminished or lost as beneficial populations decline, threatening capacity for sustainable food production (Kremen et al., 2002; Menalled et al., 2007). While individual functions and services can be maximised at relatively low levels of diversity (Perkins et al., 2014), the full importance of species-rich ecological communities in delivery of ecosystem services may become more apparent when multiple ecosystem functions are considered simultaneously (Lefcheck et al., 2015). This is the concept of ecosystem multifunctionality (Hector and Bagchi, 2007).

Pasture-based livestock production systems represent a large proportion of global agricultural land use, corresponding to more than 64% of the United Kingdom's agricultural area alone (DEFRA, 2013). In these systems, dung beetles play an important role in mediating the ecosystem service of dung decomposition through direct consumption, by incorporating dung into the soil, and by aerating the dung via tunnelling (Hanski and Cambefort, 1991). While the action of removing dung from the pasture surface has the direct benefit of allowing continued growth of the pasture sward, supporting services linked to dung removal have far-reaching benefits for the sustainability of agroecosystems

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(Beynon et al., 2015; Nichols et al., 2008). These include increased mineralisation of organic nitrogen contained in dung (Gillard, 1967; Yokoyama et al., 1991); enhanced hydrological properties of soils (Brown et al., 2010); reduced transmission of gastrointestinal parasites (Gregory et al., 2015); and reduced greenhouse gas fluxes (Penttilä et al., 2013). Dung removal (the rate at which dung is cleared from the pasture surface) is often used as the sole measure of dung beetle-mediated functioning (Beynon et al., 2012; Kaartinen et al., 2013). However, the wide variety of reproductive and behavioural strategies used by dung beetles means that dung removal rates may not adequately reflect other functions and services. The effects of dung beetle functional diversity on multiple ecosystem services have not been explored previously for temperate species.

Dung beetles are an excellent model system to explore biodiversity–ecosystem functioning relationships, as they exploit discrete and ephemeral resources, and their diversity can be manipulated experimentally at a relevant spatial scale (Beynon et al., 2012; Slade et al., 2007). To gain a better understanding of how the functional identity of dung beetles influences the provision of multiple ecosystem services, we manipulated dung beetle assemblages experimentally, holding beetle biomass constant, while varying species richness and functional diversity. In addition to the widely-studied service of dung removal, we focus on two additional ecosystem services: soil surface aeration and feeding activity by soil fauna leading to plant litter decomposition. Pasture soils are compacted by livestock and agricultural machinery, which may limit pasture productivity (Martı'nez and Zinck, 2004). Compaction may also lead to off-site impacts, where rainfall cannot percolate into the soil, and runoff may enter nearby watercourses (Alderfer and Robinson, 1947). Plant litter decomposition is a critical component of nutrient cycling (Swift et al., 1979), mediated by microbes, but accelerated by soil invertebrates (Hättenschwiler et al., 2005). Although dung is a rich source of nutrients, it is a hypoxic environment (Holter and Spangenberg, 1997): dung persisting on the pasture surface may cause hypoxia in the underlying soil, a condition known to limit the activity of soil fauna (Qualls and Richardson, 2000). Through the action of dung beetles aerating the dung, and incorporating nutrient-rich material into the soil, soil invertebrate functioning could be enhanced by the presence of dung, when subject to dung beetle activity.

2. Materials and methods

2.1. Study site

The experiment was conducted on an improved pasture at Dr Beynon's Bug Farm, St Davids, Pembrokeshire, UK (51°53′22″, 5°14′06″). The dominant plant species was rye grass *Lolium perenne*, which was sown in 2006, with white clover *Trifolium repens*. The underlying soil is part of the Moore Gate series; a well-drained, humose gritty loam in the England and Wales Soil Survey Classification (Clayden and Hollis, 1984). The field is managed under a rotational system, with land use over the past 10 years including potatoes, spring barley and short-term (~4–6 year) *Lolium perenne*-based grazing leys. At the time of the experiment, a flock of 40 Welsh Mountain ewes and their lambs grazed the field in rotation with other fields on the farm. Immediately before the experiment, the sward in the immediate experimental area was cut to a length of *c.* 1 cm and cuttings were removed by hand. Sheep were excluded from the immediate experimental area with electric fencing.

2.2. Experimental enclosures and treatments

To manipulate dung beetle assemblages, enclosures were constructed using 14 L, 35 cm diameter black buckets with the bases removed, sunk into the soil to a depth of *c.* 4 cm (Fig. 1a). Enclosures were arranged in a 5 m × 5 m grid, spaced at 1 m. One of four dung beetle assemblage treatments (three single-species treatments and one multi-species treatment) or two control treatments (beetle-free dung, and enclosures without dung or beetles) was assigned at random to each enclosure.

British dung beetles can be classified into three principal functional groups, based on their mode of exploiting dung (Doube, 1990). Dung-ovipositing endocoprids feed and lay eggs within dung, and larvae feed within dung or underlying soil. Soil-ovipositing endocoprids also feed within dung, but move to the dung-soil interface to lay their eggs, with larvae typically dispersing into the dung to feed. Paracoprid dung beetles dig tunnels in the soil below dung, creating brood chambers provisioned with dung, where eggs are laid and larvae feed. Each of the three functional groups was represented by a single species

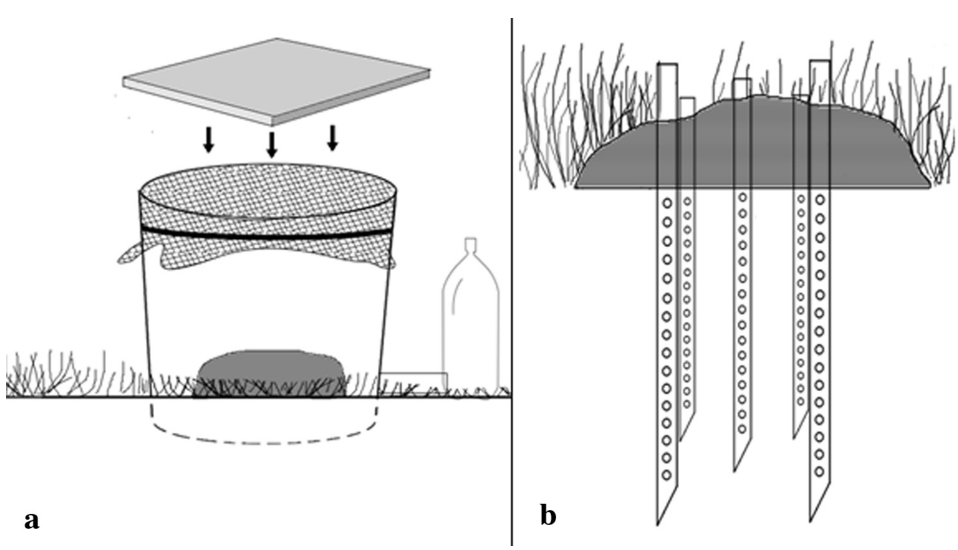

Fig. 1. Experimental setup. (a) enclosure, with emergence bottle attached. Soil fauna are able to colonise naturally from surrounding soil. (b) Placement of bait lamina strips through a dung pat. Strips are inserted to same depth in dung free controls.