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Short communication

Species-specific effects of dung beetle abundance on dung removal and leaf litter decomposition

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ABSTRACT

In grazed ecosystems, coprophagous beetles are known to play an important role in nutrient cycling, but interactions between species identity and dung beetle abundance on soil processes remain unclear. We conducted an outdoor mesocosm experiment to investigate the effects of three dung beetle species at four levels of abundance on dung incorporation into the soil. In addition we assessed indirect effects of dung beetle activity on leaf litter decomposition by microorganisms in soil. Both dung removal and leaf litter mass loss were positively correlated with initial dung beetle biomass and beetle abundance across species. However, the magnitude of beetle-induced increases in litter mass loss was very small compared to the magnitude of beetle effects on dung removal. Beetle effects on dung removal and litter decomposition also showed significant abundance × species interactions, with strongest responses observed for *Colobopterus erraticus* Linnaeus. Our findings highlight the importance of interactive effects between species identity and abundance on dung removal and provide the first demonstration of indirect dung beetle effects on leaf litter decomposition in soil.

1. Introduction

Dung beetles play an important role for soil nutrient cycling and soil structure where dung is present as a result of tunneling, dung shredding and dung burial (Yokoyama et al., 1991; Bang et al., 2005; Brown et al., 2010). Dung beetle activity is of particular interest in grazed ecosystems, where dung beetles reduce the areas covered by animal waste and contribute to the sustainability of livestock production by increasing pasture productivity and suppressing livestock parasites (Nichols et al., 2008). However, mounting evidence suggests that the diversity and abundance of dung beetles may face threats due to changes in land-use and climatic conditions (Nichols et al., 2008; Nervo et al., 2014). Understanding the linkages between dung beetle community attributes and ecosystem processes is therefore critical for the prediction of ecosystem function in a changing environment (Nichols et al., 2008; Beynon et al., 2012; Braga et al., 2013).

Dung beetles are a diverse group of insects (Scarabaeidae, Aphodiidae, Geotrupidae) which feed on animal excreta (Hanski and Cambefort, 1991). Dung beetles can be classed into three main functional groups: endocoprids (dwellers) whose larvae feed in dung pats or at the dung–soil interface, paracoprids (tunnellers) who bury brood balls in vertical tunnels under the dung pat, and telecoprids (rollers) who transfer dung away from the pat before burying brood balls under the soil surface (Hanski and Cambefort, 1991)Shredding, feeding-on and relocation of dung by dung beetles during tunneling has a direct effect on dung disappearance from the soil surface (Holter et al., 2002; Yamada et al., 2007; O'Hea et al., 2010). Moreover, dung beetle activity may have indirect effects on the decomposition of soil organic matter (OM) and plant litter fragments via beetle-induced changes in soil conditions such as aeration and soil water holding capacity (Bang et al., 2005; Brown et al., 2010), and/or stimulation of microbial biomass due to local inputs of labile carbon from dung (Bardgett et al., 1998; Hatch et al., 2000). Previous work has shown that dung beetle effects may vary depending on species composition, functional group richness and species identity (Bang et al., 2005; Slade et al., 2007; O'Hea et al., 2010; Beynon et al., 2012). Experiments with species mixtures have also shown faster dung removal in the presence of higher dung beetle abundance (Yamada et al., 2007). In theory, the magnitude of dung beetle effects may vary across species due to

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differences in beetle burrowing activity or species body mass (Holter et al., 2002; Larsen et al., 2005; Nervo et al., 2014). Indeed, recent work suggests that effects of dung beetles on ecosystem function may reflect a balance between beetle abundance, biomass and presence of species with particular attributes (small-ve large-body size) (Braga et al., 2013). However, little is known about the influence of beetle species identity on the relationship between beetle abundance and dung removal, and indirect effects of dung beetles on leaf litter decomposition have never been assessed.

Here we report a mesocosm study on the interactive effects of dung beetle species identity and beetle abundance on dung removal and decomposition of leaf litter in soil beneath dung pats. The study was conducted using three co-occurring dung beetle species which bury dung beneath the dung pat: *Colobopterus erraticus* (Linnaeus, 1758), *Caccobius schreberi* (Linnaeus, 1758) and *Onthophagus vacca* (Linnaeus, 1767). *C. erraticus* and *C. schreberi* are small-sized beetles (mean dry body mass of eight and seven mg respectively), whereas *O. vacca* is a large sized-species (mean body mass 41 mg) (Lumaret and Kirk, 1987). These three species are commonly found in the French Mediterranean region during the spring period (Lumaret and Kirk, 1987). We hypothesized that: (i) dung removal by dung beetles increases with increasing beetle biomass and abundance; (ii) dung removal by dung beetles varies depending on beetle species; (iii) high dung beetle biomass and abundance accelerates leaf litter decomposition in soil.

2. Materials and methods

In April 2012, 51 experimental units were established in the CNRS-CEFE experimental field platform in Montpellier, France (43°38′16N, 3°51′41, elevation 58 m). Each experimental unit comprised of a plastic pot (15 cm diameter, 25 cm deep) filled with a mix of fersiallitic brown Mediterranean soil and sand ($pH_{H2O} = 6.8$; 0.3% N for the soil/sand mix); the soil/sand mix was used for logistical reasons to be able to clearly distinguish dung, beetles and brood balls from the soil medium at the end of the study. Pots were placed in holes in the ground such that the surface of the pot was flush with the soil surface, and enclosed above-ground using 0.2 mm mesh cages (25 × 25 × 15 cm) nailed to the ground immediately adjacent to the buried pot. These cages were used to avoid i) dispersal of experimental beetles away from the pots and ii) colonization of the pots by macro- and meso-invertebrates from the surrounding area.

Litter decomposition was assessed following Bloor and Bardgett (2012) using 5 × 5 cm litterbags (25 μm mesh; ANKOM Technology, Macedon, NY, USA) filled with 0.5 g of standardised leaf litter (50:50 mix of *Festuca rubra* and *Lolium perenne* senescent leaf material, 1.6% N, 28C:N). Litter from each plant species was dried (60 °C for 48 h), finely cut (1 mm), and combined to produce the standardised litter mix with equal dry mass of each plant species. One litter bag was inserted vertically into the soil of each pot to a depth of 5 cm, and 500 g of fresh, homogenised cow dung was then placed on the soil surface of each pot (dung composition 85.7% H_2O, 2.7% N, 15.6C:N, collected from a nearby dairy farm). Dung was uncontaminated by antibiotics or anthelmintics since no veterinary medical products were administered to animals for at least 100 days before dung was collected.

Adult dung beetles for use in the study were collected locally from grazed meadows using dung-baited pitfall traps, identified to species, sexed and stored in cool conditions for three weeks prior to the experiment. Four beetle density treatments were established per species. Beetles of *C. erraticus* Linnaeus, *C. schreberi* Linnaeus and *O. vacca* Linnaeus were added to mesocosms as 50:50 male:female pairs at densities of either two, four, eight or 12 individuals, consistent with variation in dung beetle abundance observed in dung pats under natural conditions (Hanski and Cambefort, 1991). These four density treatments were replicated four times per species (total of 16 experimental units per species). Three remaining experimental units were kept as beetle-free controls. All experimental units were then left under natural rainfall conditions for five months.

In September 2012, beetles were removed by hand from the experimental units. All remaining dung on the soil surface was collected, dried (48 h, 60 °C) and weighed to determine residual dung dry mass. Organic matter content of this remaining dung was determined from loss of weight of dried dung samples after being ashed at 500 °C for 12 h. Dung removal was calculated as the proportion of OM lost from the start to the end of the experiment following Holter (1979). Litter bags were retrieved from the soil, cleaned and dried (48 h, 60 °C) before being weighed to determine litter mass loss during the five-month incubation period. Values for both dung removal and litter mass loss in the presence of beetles were corrected by values obtained in beetle-free controls (i.e. treatment values − mean control value) to separate out dung beetle effects. Effects of species identity and beetle abundance were assessed using two-way analysis of covariance (ANCOVA) with beetle species as a fixed factor and initial beetle abundance as a quantitative, independent variable, following Zar (1998). Effects of beetle biomass on dung removal and litter decomposition were examined using simple linear regression, and estimations of beetle biomass were based on mean beetle dry mass and initial beetle numbers. All statistical analyses were carried out using Statgraphics Plus 4.1 (Statistical Graphics Corp., Rockville, Maryland, USA).

3. Results

Mean dung removal due to dung beetle presence ranged from 3.2 to 23.0% across species and abundance treatments over the five-month incubation period. Dung removal showed a positive relationship with dung beetle biomass estimated at the start of the study ($R^2 = 0.56$, $P < 0.01$; Fig. 1). In general, rates of dung removal increased with increasing beetle abundance across species treatments (Table 1, Fig. 2). However, dung removal also showed significant species × abundance interactions (Table 1); dung removal increased with more individuals of *C. erraticus*, but showed no response to increasing abundance of *C. schreberi* or *O. vacca* ($R^2 = 19.8$, $P < 0.05$; Fig. 2).

Leaf litter bags showed significant mass loss during the study (mean mass loss of 40.1% across treatments and controls), but very little of the litter mass loss in the beetle treatments could be directly attributed to beetle presence due to high litter mass loss in the control pots (Fig. 1). Nevertheless, leaf litter decomposition showed a positive relationship with initial beetle biomass ($R^2 = 0.32$, $P < 0.05$; Fig. 1) and increased with increasing beetle abundance across species treatments (Table 1, Fig. 2). As with dung removal, leaf litter decomposition showed significant species × abundance interactions (Table 1). Litter mass loss increased in the presence of more *C. erraticus* individuals ($R^2 = 0.88$, $P < 0.05$; Fig. 2) but was unaffected by increasing abundance of *C. schreberi*. Litter decomposition showed a marginally significant positive relationship with increasing *O. vacca* abundance ($P = 0.08$; Fig. 2).

4. Discussion

The role of community attributes for ecosystem function has faced considerable interest in recent years due to growing concerns over altered species abundance and diversity patterns under global change (see Larsen et al., 2005; Slade et al., 2007; Nichols et al.,