Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness

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ABSTRACT

Intensive management practices have been widely shown to reduce the diversity and abundance of insects in agricultural landscapes. This loss has attracted considerable public and scientific interest, owing partially to the importance of insects in supporting ecosystem functions. The relative importance of diversity and abundance in underpinning ecosystem functioning, however, has not been widely explored. We examined the relative importance of diversity and abundance in ecosystem functioning using a model system of three widespread species of dung beetle (Coleoptera: Scarabaeoidea). We used a design that manipulated species richness, while also standardizing dung beetle abundance at two levels. We predicted that individual species would contribute unequally to ecosystem functioning, functioning in multi-species assemblages could be reliably predicted from single-species assemblages, and that loss of abundance would more strongly affect functioning than loss of diversity. Comparisons of functioning among three species showed that individual species contributed unequally to dung removal. In most cases multi-species assemblages provided higher levels of dung removal than predicted by single-species assemblages, demonstrating evidence of complementarity. The average effect of species richness loss had no significant effect on dung removal. In contrast a 33% loss of insect abundance corresponded to a 29% reduction in dung removal. Our work provides empirical evidence that loss of insect abundance, a widely occurring response to agricultural intensification, can have stronger consequences for ecosystem functioning than reductions in species richness. Further efforts should confirm whether this relationship is consistent across other ecosystem functions. Should this be observed, ecosystem functioning arguments could be useful in motivating agricultural producers to participate in practices such as agri-environment schemes which have potential to simultaneously conserve the diversity and abundance of insects in agroecosystems.

1. Introduction

Determining the contribution of biodiversity to ecosystem functioning is a fundamental ecological question that has been intensively studied over the past twenty-five years (Isbell et al., 2017). Typically this relationship has been tested by experimentally assembling communities with varying levels of species richness; evidence overwhelmingly supports a theory where ecosystems with greater species richness (e.g. higher biodiversity) provide higher levels of functioning relative to ecosystems with lower biodiversity (Hooper et al., 2005).

Two principal mechanisms are thought to account for positive relationships between biodiversity and ecosystem functioning. First, ecosystems containing a greater number of species are more likely, by chance, to include particularly efficient species. This is known as the 'sampling effect', a phenomenon where higher resource utilization relies on species identity, rather than other properties of biologically diverse ecosystems (Wardle, 1999). Second, individual species use

resources in dissimilar ways such that total resource use is more complete in communities with higher biodiversity; this is known as the 'complementarity effect' (Loreau and Hector, 2001).

The relationship between biodiversity and ecosystem functioning is highly relevant to agriculture, which depends on numerous ecosystem functions to underpin production (Zhang et al., 2007). Many of these functions – including pollination, biological pest control, and dung decomposition – are supported by insects (Noriega et al., 2018). Intensive management practices have been widely shown to drive losses of insect biodiversity within agricultural landscapes (Tuck et al., 2014) and in some cases these losses may have consequences for functioning. For example, lower species richness levels of predaceous insects, bees, and dung beetles have been linked to losses of biological pest control (Snyder et al., 2006), crop pollination (Garibaldi et al., 2013), and pasture productivity (Manning et al., 2017b), respectively. The loss of species can be particularly problematic when the most sensitive species also provide the highest levels of ecosystem functioning (Piccini et al.,

2018).

While loss of ecosystem function often maps closely to biodiversity losses, ecosystem functioning can be lost or gained in ways that do not involve any changes to species richness levels (Spaak et al., 2017). One such change with known relevance to insect-mediated ecosystem functions is changes in abundance. For example, Winfree et al. (2015) found crop pollination is predominately driven by the abundance of common species, while also finding that the overall richness of bee communities is a poor predictor of functioning. This has applied relevance within the context of agricultural production, because like diversity, insect abundance also typically responds negatively to agricultural intensification (Bengtsson et al., 2005).

Here we examined the relative consequences of species loss and abundance declines in explaining ecosystem functioning. We approached this problem using a mesocosm experiment that included three widespread species of dung beetle (Coleoptera: Scarabaeoidea), and the ecosystem function of dung removal. Most dung beetle species, including those used in our experiment, are obligate coprophages and feed on dung as both larvae and adults (Hanski and Cambefort, 1991). Dung beetles routinely colonize and use the dung of livestock grazing in pastures. Burial and consumption of livestock dung supports numerous ecosystem functions: enhancing primary productivity (Manning et al., 2017b), decreasing survival of gastrointestinal parasites (Sands and Wall, 2017), and reducing greenhouse gas emissions from cattle farming (Slade et al., 2016). Dung beetles are well known to respond negatively to intensive farming practices (Hutton and Giller, 2003), which include non-target exposure to veterinary anthelmintics (Beynon et al., 2012) and loss of thermal refuges associated with landscape simplification (Hutton and Giller, 2003).

We used a fully-factorial design, where species richness varied but beetle biomass did not, to test the importance of diversity in explaining ecosystem functioning. We replicated this design at two different beetle densities, which allowed us to test the effects of diversity and abundance in explaining ecosystem functioning (dung removal). Additionally, we tested whether individual species provided varying levels of functioning and determined whether estimates of functioning in multi-species assemblages could be reliably predicted from single-species assemblages.

We predicted that:

a) aIndividual species would contribute unequally to ecosystem functioning;
b) There would be little complementarity among species: single-species assemblages would reliably predict multi-species assemblages; and
c) Loss of abundance would more strongly influence ecosystem functioning than loss of species.

2. Methods

2.1. Field collection and identification of experimental species

Live dung beetles were hand-collected from 2 to 10 July on pastures grazed by horses, sheep and cattle near Truro and Canning, Nova Scotia, Canada. The resident dung fauna community was dominated by introduced Palearctic species, which were identified to species level using Jessop (1986). The species *Aphodius fossor* L., *Aphodius erraticus* L., and *Onthophagus nuchicornis* L. were the dominant species across five sites and were selected for experiments. Other dung beetle species recorded during sampling included: *Onthophagus hectate* Panzer, *Geotrupes stercorarius* L., *Aphodius prodromus* Brahm and *Aphodius fimetarius* L., but these were much rarer, representing cumulatively < 5% of overall capture during the sampling period. We brought beetles back to the lab, sorted them by species, and housed conspecific males and females together in ventilated plastic containers (27 × 38 × 10 cm) filled halfway with moist Promix® potting medium. Prior to beginning the experiment, beetles were fed dung from dairy cows, which had not been treated with any anthelmintics for the past four months.

2.2. Mesocosm design

The experiment was conducted using mesocosms constructed from white 11.4 L high density polyethylene tubs (24.75 cm deep, 30.5 cm high). Each tub had a pink low-density polyethelyne lid, where an inner circle of 15 cm d was removed and replaced with a 1 mm gauge black vinyl window screen to allow ventilation. Each tub was filled to a depth of 20 cm with a 7:3 (v:v) combination of Promix and silica sand. We evenly scattered 5 mL of perennial ryegrass seed (*Lolium perenne* L.) onto the soil surface of each mesocosm on 15 May. Mesocosms were left uncovered and placed in a greenhouse until beginning the experiment to allow the ryegrass to establish. Mesocosms were watered daily and ryegrass was clipped to 3 cm height on a weekly basis. Bare patches were reseeded on 30 May and 12 June.

Dung used in the experiment was obtained from a herd of Holstein dairy cows at Dalhousie Agricultural Campus. Cows had been feeding on pasture for ten days, with diet supplemented with hay, corn silage, and feed concentrate during the evenings. Cows had not been treated with any anti-parasitic products for the previous four months. Fresh dung (< 1 h old) was collected before it was colonized by flies. Dung was stored in 11.4 L plastic buckets and frozen for five weeks at −22 °C to kill any invertebrates which might have colonized prior to collection.

We removed the frozen dung from the freezer on 12 July and thawed it for 24 h. On 13 July dung was homogenized in a large plastic tote using a spade. We allocated 550 g allotments of cow dung to each mesocosm. Dung was formed into an artificial dung pat using a 15 cm d plastic circular frame.

2.3. Dung beetle assemblages

We used a factorial design when making the experimental dung beetle assemblages. Following the approach of Beynon et al. (2012), all assemblages were standardized using the mean dry biomass (mg) of each species reported in previous studies (Table 1). Evenly distributing the estimated biomass among all species, we tested all possible combinations of the three dung beetles (Table 1). Each level of species richness was replicated n = 9 times. When multiple community combinations were possible from a single species richness level, each was tested an equal number of times (n = 3). Because it was not possible to reliably determine the sex of *A. erraticus*, we assumed random allocation of beetles to treatments would approximate a 1:1 male to female ratio. Male and females were readily discerned for *O. nuchicornis* and *A.*

Table 1
Composition of experimental dung beetle assemblages. Richness of assemblages varied from 1 to 3 species. When for a given richness level multiple permutations were possible (e.g. 2-species assemblages), the nine replicates were equally subdivided among the three possibilities (AB, BC, BC). Table values indicate dung beetle abundance, which was set to targets of 106 ± 1 mg and 159 ± 1 mg of beetles per mesocosm in the low and high treatment respectively.

Abundance	Species	Mean individual dry mass (mg)	Beetle Assemblage						
			A	B	C	AB	AC	BC	ABC
Low	*A. erraticus* (A)	9.0[a]	12	–	–	6	6	–	4
	O. nuchicornis (B)	7.7[b]	–	14	–	7	–	7	5
	A. fossor (C)	26.1[c]	–	–	4	–	2	2	1
High	*A. erraticus*	9.0	18	–	–	9	9	–	6
	O. nuchicornis	7.7	–	21	–	10	–	10	7
	A. fossor	26.1	–	–	6	–	3	3	2

Estimate of dry biomass from Gittings and Giller (1997)[a], Sullivan et al. (2017)[b], Roslin and Koivunen (2001)[c].