

Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems

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Summary

1. Many studies document high levels of functional redundancy in ecosystems, suggesting that species extinctions will not be detrimental to ecosystem functions and services. However, apparently redundant taxa may prove critical for sustaining ecosystem functions and services in the context of environmental perturbations.

2. Dung beetles (Coleoptera:Scarabaeidae) provide a valuable ecosystem service in temperate agro-ecosystems by increasing rates of dung decomposition and nutrient cycling. However, there is concern that these services may be negatively affected by changes in species richness and composition due to changes in pasture management and negative effects of anthelmintics used to control livestock parasites.

3. We used a mesocosm experiment to investigate the functional importance of dung beetle species richness in a system perturbed by the anthelmintic, ivermectin. We varied dung beetle species richness within three functional groups in factorial combination with ivermectin treatment.

4. In the short term (1–4 weeks), multi-species dung beetle assemblages achieved higher decomposition rates than monocultures, but only in ivermectin-treated dung. Varying species-specific sensitivities to ivermectin meant that species-rich assemblages sustained ecosystem functioning in the context of this anthropogenic perturbation.

5. Over the longer term (36 weeks), there was a significant, positive effect of species richness on dung decomposition in both ivermectin-treated and untreated dung, underlining the functional importance of maintaining a species-rich dung processing community even in the absence of perturbations to the system.

6. *Synthesis and applications.* The interacting effects of dung beetle species richness and ivermectin highlight the importance of maintaining diverse assemblages in the face of anthropogenic perturbations and suggest that apparent functional redundancy of species in agro-ecosystems should be interpreted cautiously. Furthermore, different farm management practices (e.g. pesticide use and fragmentation of habitats) may have consequences for ecosystem functions and services that exceed the effects of each when considered in isolation.

Key-words: biodiversity, decomposition, ivermectin, mesocosm, perturbation, pesticide, redundancy

Introduction

Species-rich communities have been shown to deliver enhanced ecosystem functions and services in both natural and human-modified ecosystems (e.g. Larsen, Williams &

Kremen 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006; Duffy 2009). However, the biodiversity–ecosystem functioning literature is dominated by studies of plants and microbe communities, and relatively few studies have considered terrestrial animal communities (Peh & Lewis 2012). Furthermore, few studies have considered the form of the relationship between richness and function when a system is disturbed. Many biodiversity–ecosystem func-

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tioning relationships appear to be saturating, suggesting species redundancy at moderate levels of species richness. However, high species richness may be crucial for sustaining functions and services in the event of perturbations or changing environmental conditions (Reich *et al.* 2001; Duffy 2009).

Here, we investigate the relationship between species richness and the ecosystem function of dung decomposition by dung beetles (Coleoptera: Scarabaeidae) in a temperate grassland agro-ecosystem, in the context of perturbation by a widely used pesticide. Dung-associated invertebrates also include a variety of other beetles (Coleoptera: Hydrophilidae, Histeridae and Staphylinidae), flies (Diptera), parasitic wasps (Hymenoptera), earthworms and springtails (Collembola). However, dung beetles are considered among the most important facilitators of dung decomposition in a variety of ecosystems, including agricultural grasslands (Gittings, Giller & Stakelum 1994; Lee & Wall 2006) and provide a widely cited example of ecosystem service provision. For example, dung beetles save the US cattle industry an estimated \$380 million annually (Losey & Vaughan 2006) by rapidly incorporating nutrient-rich organic matter into the soil, reducing the need for artificial fertilizers and reducing pasture fouling (Stevenson & Dindal 1987; Lumaret & Kadiri 1995). They also help reduce the spread of parasites (Gronvold *et al.* 1992). In the UK, dung decomposition in agricultural grasslands has been identified as a key ecosystem service of high policy relevance (Sutherland *et al.* 2006).

In agro-ecosystems, reduced dung beetle species richness has been shown to arise from agricultural intensification (Hutton & Giller 2003) and fragmentation of habitats (Roslin & Koivunen 2001). There are also concerns that the widespread practice of treating livestock with anthelmintic drugs such as ivermectin will negatively affect dung beetle assemblages (Hempel *et al.* 2006; Boxall *et al.* 2007), and associated rates of dung decomposition (Wall & Strong 1987; Sommer & Bibby 2002). Ivermectin could affect dung decomposition either by altering the biomass or species richness of dung beetle assemblages or by sublethal effects on the efficiency of component individuals and species. There is limited research investigating the effects of anthelmintics on interactions among species (Floate & Fox 1999; Edwards 2002; Floate 2006; Jensen, Diao & Hansen 2009). This gap in knowledge restricts our ability to understand the functional consequences of ivermectin use for diverse, multi-species assemblages.

Here, we use a mesocosm experiment to investigate whether dung beetle species richness within functional groups affects rates of dung decomposition, whether functional groups of dung beetles vary in their functional efficiency and whether the relationship between species richness and decomposition is altered by perturbation of the system with ivermectin. To understand the mechanisms driving our results, we also explore the effects of ivermectin treatment on adult beetle survival and offspring emergence (a function of adult survival and fecundity and offspring

survival). We consider the implications of functional group and species richness effects in both perturbed (with ivermectin) and unperturbed systems for the sustainability of agricultural practices in temperate agro-ecosystems.

Materials and methods

COLLECTION AND IDENTIFICATION OF FOCAL SPECIES

To establish experimental treatments, live dung beetles were collected by hand and using dung-baited pitfall trapping in sites in southern and western UK during April–June 2010. Dung beetles were identified using Jessop (1986) and classified into three functional groups: (A) soil-ovipositing endocoprids, (B) dung-ovipositing endocoprids and (C) paracoprids, following Doube (1990) and based on life-history traits from Landin (1961) and Finn & Gittings (2003). Adult beetles feed on the liquid fraction of the dung, while larvae feed on solid particles. Adult dung-ovipositing endocoprid beetles tunnel within the dung pat and eggs are laid within the pat. Soil-ovipositing endocoprid adults also feed within the pat but their eggs are laid in the underlying or surrounding soil and larvae move to the pat. Paracoprid species dig brood chambers in the soil below the pat and provision them with dung. Eggs are laid and larvae develop within these brood chambers.

Beetles were housed in mixed-sex containers in a well-lit, ventilated shed until the start of the experiment. They were fed with fresh cattle dung from grass-fed animals that had not been treated with anthelmintics for >6 months. Species included in the experiments were randomly chosen from those collected in sufficient numbers.

MESOCOSM EXPERIMENTS

Dung for the mesocosm experiments was obtained from a group of 12 mature, organic Welsh Black cattle at Penweathers Farm, St. Davids, Wales (51°53'7.5", 5°15'48.9"). The cattle had been wintered outdoors and had not been treated with anthelmintics for at least 2 years. Dung quality can vary depending on the pastures grazed by cattle (Beynon *et al.* 2012). To avoid confounding pasture-to-pasture differences with anthelmintic treatment, dung from the same group of cattle grazing the same pasture, but collected pre- and post-treatment, was used in the mesocosm experiments. Pre-treatment fresh dung (<6 h old) was collected on the day before treatment and on the day of treatment (10 May 2010). Cattle were then treated with an ivermectin pour-on (Animec™) at the recommended dose of 10 mL kg⁻¹ live mass. Post-treatment dung was collected one and 2 days after treatment, corresponding to peak faecal excretion of pour-on ivermectin (Sommer & Steffansen 1993; Herd, Sams & Ashcraft 1996). One- and 2-day old dung was combined 1 : 1 by mass. Dung was frozen to -20 °C until required, when it was thawed at ambient temperatures. Pre-treatment and post-treatment dung samples were separately homogenized using a mortar mixer.

Experimental mesocosms were constructed using 14-L, 35-cm diameter cylindrical buckets. Three 2-cm-diameter drainage holes (covered with 0.7-mm plastic mesh) were drilled in the base and a 2-cm-diameter hole for fitting an emergence trap was drilled at a height of 16 cm and sealed with tape. Each mesocosm was filled to a depth of c. 13 cm with hand-compressed sandy loam topsoil and topped with a disc of *Lolium perenne* Linnaeus turf (c. 3 cm

thick), which was free from macro-invertebrates (S. Beynon, unpublished data). Mesocosms were allocated to random positions on an 8 × 7 m rectangular grid, spaced at 1 m (Fig. S1, Supporting Information) in an unimproved meadow at Lower Moor, St Davids, Wales (51°52'30.5"N, 5°16'38.5"W).

The effects of varying species richness within functional groups on rates of dung decomposition were explored in synthetically assembled dung beetle assemblages. The experiment included one, two or three species per functional group per replicate while holding total dung beetle biomass constant (Table 1). Mesocosm beetle biomass (156.6 mg dry mass) was set by the monoculture biomass ($n = 6$) of the heaviest species, *Aphodius fossor* Linnaeus (26.10 mg dry mass). The biomass of beetles used in the experiment per unit dung mass was equivalent to that observed under natural field conditions in the UK (S. Beynon, pers. obs.). Where fewer than five individuals per species were allocated to a mesocosm, beetles were sexed to ensure both females and males were represented. While large paracoprids (e.g. Geotrupidae) can contribute disproportionately to dung removal (Slade *et al.* 2007; Rosenlew & Roslin 2008), we excluded them from the experiment. Biomass discrepancies made the inclusion of geotrupid species impractical, for example, a single *Geotrupes spiniger* is more than 88 times the mass of one *Aphodius granarius* (Gittings & Giller 1997; Rosenlew & Roslin 2008). Thus, restricting the study to smaller species allowed us to investigate more subtle biodiversity–ecosystem functioning relationships, while retaining realistic assemblages of beetles in our treatments.

As there were too many permutations to study all possible species combinations, species identities for the one- and two-species mesocosms were drawn at random from the pool of available species so that a randomly selected one-, two- and three-species combination was included for each functional group (Table 2). Each mixture was replicated three times. This design was repeated using either ivermectin-treated or untreated dung, giving a total of 54 mesocosms containing 1140 beetles. While this design leaves many species combinations unstudied, it allows us to quantify the role of species richness, independent of functional group richness. Five beetle-free mesocosms per anthelmintic treatment (ivermectin or control) were also included to check for direct effects of dung treatment on decomposition.

To assess species-specific survival due to ivermectin, a second experiment was established using replicated single-species meso-

cosms of all species included in the first experiment. Total mesocosm beetle dry biomass was again 156.6 mg. Mesocosms for each species were replicated with either ivermectin or control dung ($n = 3$ for both treatments). Monoculture mesocosms included in the species richness experiment were also used in the analyses of this experiment. Thus, 36 additional mesocosms containing 576 additional beetles were included, giving a total of 54 mesocosms containing 1062 beetles for analyses.

At the start of both experiments (7 June 2010), a single 600-g, 18-cm-diameter dung pat, made from the collected dung, was placed in each mesocosm, supported by a 25-cm-diameter circle of 2-cm wire mesh. The appropriate number of beetles was then added. Anthelmintic treatments (ivermectin or control) and beetle treatments were randomly allocated to mesocosms. Mesocosms were covered with fine plastic mesh, secured with elastic cord. Grass within the mesocosm was cut every 2 weeks (June–November 2010) to c. 4 cm.

For the first 4 weeks of the experiments, pats were lifted from the mesocosms on the wire mesh and weighed weekly to calculate 'short-term' decomposition rates corresponding to the main period of beetle feeding and nesting activity (Landin 1959, 1961). Pats were then re-weighed after 36 weeks, in March 2011 (corresponding to the start of the next grazing season). This final 'long-term' measure is relevant from an applied perspective, as any dung remaining at the start of the following grazing season would reduce the area of grass available for grazing and may retard palatable spring grass growth (Bang *et al.* 2005). Wet masses were used to measure dung decomposition as they allow repeated, non-destructive sampling and provide a reliable measure of decomposition rates (Wall & Strong 1987; Slade *et al.* 2007).

In both experiments, beetle survival was assessed using emergence traps at 2.5 weeks, when adult beetles naturally start to leave the dung (Landin 1959, 1961; Gittings & Giller 1997). Tape covering the exit holes was removed and clear plastic collecting bottles were connected using a clear plastic tube of 4 cm length and 2 cm diameter. At this time, the fine mesh covering the mesocosm was replaced with light-reducing black material to encourage beetles to move into the collecting tube and bottle. The fine mesh was replaced in November, once all beetles had emerged, and black material again replaced the fine mesh in February 2011, for collection of offspring emerging the following year. Emergence traps were removed, and the experiment terminated in

Table 1. Experimental beetle species

Species	Functional group	Individual dry mass (mg)	Species richness experimental treatments		
			1	2	3
<i>Aphodius ater</i> De Geer	Dung-ovipositing endocoprid	5.43*	29	14	10
<i>Aphodius granarius</i> Linnaeus	Dung-ovipositing endocoprid	2.98*	53	0	18
<i>Aphodius pedellus</i> De Geer	Dung-ovipositing endocoprid	9.40†	17	8	6
<i>Aphodius depressus</i> Kugelann	Soil-ovipositing endocoprid	9.10, $n = 21^‡$	17	9	6
<i>Aphodius fossor</i> Linnaeus	Soil-ovipositing endocoprid	26.10†	6	3	2
<i>Aphodius luridus</i> Fabricius	Soil-ovipositing endocoprid	15.69, $n = 11^‡$	10	0	3
<i>Aphodius erraticus</i> Linnaeus	Paracoprid	9.01*	17	0	6
<i>Onthophagus joannae</i> Goljan	Paracoprid	9.47, $n = 10^‡$	17	8	6
<i>Onthophagus similis</i> Scriba	Paracoprid	13.87, $n = 11^‡$	11	6	4

*Biomass taken from Gittings & Giller (1997).

†Biomass taken from Roslin & Koivunen (2001).

‡Biomass obtained from dry masses of individual beetles collected in 2010.

Table 2. Mesocosm species identities.

Functional group	Three-species mesocosm	Two-species mesocosm	Monoculture mesocosm
Dung-ovipositing endocoprid	<i>Aphodius ater</i> , <i>Aphodius granarius</i> , <i>Aphodius pedellus</i>	<i>Aphodius ater</i> & <i>Aphodius pedellus</i>	<i>Aphodius granarius</i>
Soil-ovipositing endocoprid	<i>Aphodius depressus</i> , <i>Aphodius fossor</i> , <i>Aphodius luridus</i>	<i>Aphodius depressus</i> & <i>Aphodius fossor</i>	<i>Aphodius depressus</i>
Paracoprid	<i>Aphodius erraticus</i> , <i>Onthophagus joannae</i> , <i>Onthophagus similis</i>	<i>Onthophagus joannae</i> & <i>Onthophagus similis</i>	<i>Onthophagus similis</i>

November 2011. A measure of tibial wear (Tyndale-Biscoe 1978) was used to separate the original beetles used to establish the experiment from their offspring. Fitting emergence traps also ensured that adult beetles were not artificially forced to inhabit pats that they would leave under natural conditions.

DATA ANALYSIS

Two measures of decomposition were analysed separately: decomposition rate over the first 4 weeks of the experiment, and dung wet mass removed at 36 weeks. \log_{10} -transformed dung pat masses over the first 4 weeks were regressed against time for each replicate, and the fitted slope values were used as a measure of decomposition rate. These log-linear regressions consistently provided the best-fitting description of the relationship between pat mass and time, with adjusted R^2 values ranging from 0.884 to 0.996. Species richness effects on dung decomposition were assessed by comparing monocultures, two-species polycultures and three-species polycultures of each functional group. Each measure of decomposition was modelled as a function of anthelmintic treatment, functional group and species richness, with all response variables treated as categorical.

The effect of ivermectin on total adult beetle survival per mesocosm was assessed with logistic regression (generalized linear models with binomial errors). Adult survival was taken as the proportion of initial adult beetles emerging from mesocosms within 6 weeks of the start of the experiment. Ivermectin impacts on offspring emergence (the number of emerging offspring) were analysed with generalized linear models (with Poisson errors) following Warton & Hui (2011). We checked for overdispersion in all cases, with quasipoisson or quasibinomial errors used where overdispersion was evident. Species-specific adult survival and offspring emergence in monoculture (where there were essentially 15 independent experiments) were modelled separately with generalized linear models as a function of anthelmintic treatment, which was treated as a categorical variable.

The two measures of performance analysed (adult survival and offspring emergence, which is a function of adult survival and fecundity plus offspring survival) as well as the two measures of dung decomposition (short-term decomposition rate and long-term decomposition) are not completely independent. However, we consider that analysing the suite of responses allows us to document more fully the potential effects of ivermectin on dung beetle assemblages and associated ecosystem services.

Following model criticism, linear models were used in all analyses measuring dung decomposition. All interaction terms were fitted, and model simplification was carried out using Akaike's Information Criterion (AIC) to test the goodness-of-fit of the model. Where changes were non-significant, interactions or

variables were dropped until the minimum adequate model was obtained (Crawley 2007). *Post hoc* treatment contrast coefficients and the Tukey's HSD (Honestly Significant Differences) test were used to explore significant results. Data were analysed using the statistical package R 2.10.0 (R Development Core Team 2006).

Results

Initial analyses of the beetle-free controls confirmed that ivermectin-treated and untreated dung did not differ significantly for 1–4 week decomposition rate (\log_{10} -transformed, $F_{1,8} = 0.84$, $P = 0.387$) or dung mass removed at 36 weeks ($F_{1,8} = 1.90$, $P = 0.205$). Beetle-free controls were therefore excluded from further analyses.

DECOMPOSITION

Species richness effects on short-term (1–4 weeks) decomposition rates were influenced by ivermectin, giving a significant 'species richness \times ivermectin' interaction ($F_{2,46} = 6.84$, $P = 0.003$; Fig. 1a). In ivermectin-treated dung, decomposition showed a positive relationship with species richness, with three-species dung beetle assemblages achieving faster decomposition rates than two-species assemblages or monocultures. This effect was most pronounced in paracoprids. There was no such relationship in control dung. Functional groups varied significantly in their functional contribution irrespective of ivermectin treatment ($F_{2,46} = 11.35$, $P < 0.001$): paracoprids contributed disproportionately to dung decomposition, with decomposition rate faster for paracoprids than either endocoprid group.

After 36 weeks (Fig. 1b), dung mass was affected by species richness ($F_{2,50} = 8.53$, $P < 0.001$) irrespective of ivermectin treatment. In most cases, monocultures had removed less dung than both two- and three-species polycultures. Ivermectin pats were heavier than control pats, but not significantly so ($F_{1,50} = 3.44$, $P = 0.070$), and functional groups no longer differed in functional efficiency.

BEETLE SURVIVAL AND REPRODUCTION

There were species-specific effects of ivermectin on adult beetle survival (Fig. 2a). Adult survival was significantly reduced by ivermectin for *Aphodius erraticus* Linnaeus

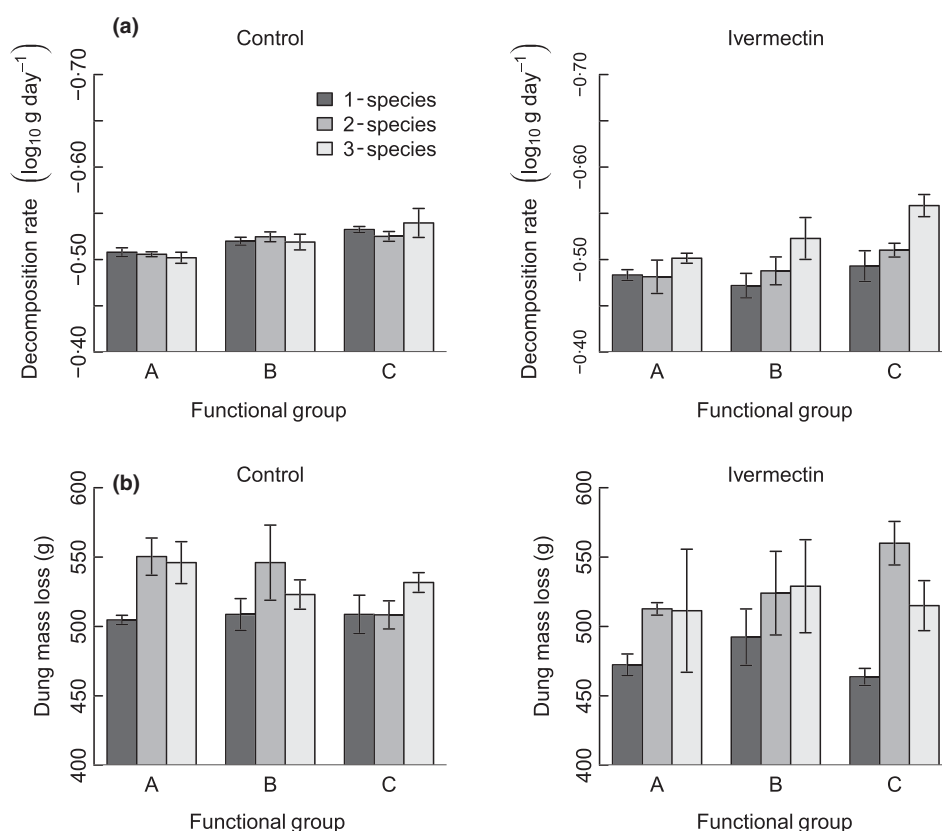


Fig. 1. Values for (a) decomposition rate (see text for method used to calculate decomposition rate), and (b) dung mass loss at 36 weeks for control and ivermectin dung in relation to species richness within each functional group. Bars are estimated means (and standard errors). Functional groups are A: dung-ovipositing endocoprids, B: soil-ovipositing endocoprids and C: paracoprids.

($\chi^2_1 = 20.95$, $P < 0.001$) and *Onthophagus similis* Scriba ($\chi^2_1 = 54.40$, $P < 0.001$). However, ivermectin significantly increased adult survival for *Aphodius depressus* Kugelann ($\chi^2_1 = 4.45$, $P = 0.035$). There were also species-specific effects of ivermectin on offspring emergence (Fig. 2b). In comparison with controls, significantly fewer offspring emerged from the ivermectin treatment for *A. erraticus* ($\chi^2_1 = 47.32$, $P < 0.001$), *A. fossor* ($\chi^2_1 = 19.41$, $P = 0.018$), *Onthophagus joannae* Goljan ($\chi^2_1 = 3.74$, $P = 0.040$) and *O. similis* ($\chi^2_1 = 34.14$, $P < 0.001$).

Discussion

SPECIES RICHNESS EFFECTS

Our experiments enable us to quantify the contributions of species richness and functional group identity to the ecosystem function and service of dung decomposition and to assess how these relationships are affected if the system is perturbed by a widely used anthelmintic, ivermectin. Over the first 4 weeks of the experiment, a positive species richness effect on functioning was only found in ivermectin-treated dung. This suggests that short-term dung decomposition is not influenced by species richness under normal conditions but that under perturbation, varying

species-specific sensitivities to ivermectin allow ecosystem functioning to be maintained in high richness assemblages. For example, within the paracoprid functional group, multi-species assemblages did not perform any better than a monoculture of *O. similis* in the absence of perturbation, suggesting species redundancy. However, when the system was disturbed by the addition of ivermectin, the survival of *O. similis* was significantly decreased, and the functional importance of the two other paracoprid species (which were less affected or unaffected as adults) became apparent. These results highlight the risk that the role of species richness in sustaining ecosystem functions and services will be underestimated in short-term studies under a single set of environmental conditions, and in the absence of environmental perturbations.

In the long-term (36 weeks), the experiments revealed a positive species richness effect on dung decomposition, with neither ivermectin nor functional group affecting decomposition significantly. Thus, species that appear to be redundant in short-term studies may prove functionally important over longer timescales. However, the magnitude of the species richness effect on mass loss overall was small (mean \pm standard error of dung mass loss: one-species = 491.72 ± 5.94 g, two-species = 533.56 ± 8.09 g, three-species = 526.00 ± 9.08 g), and thus, the practical significance of these results

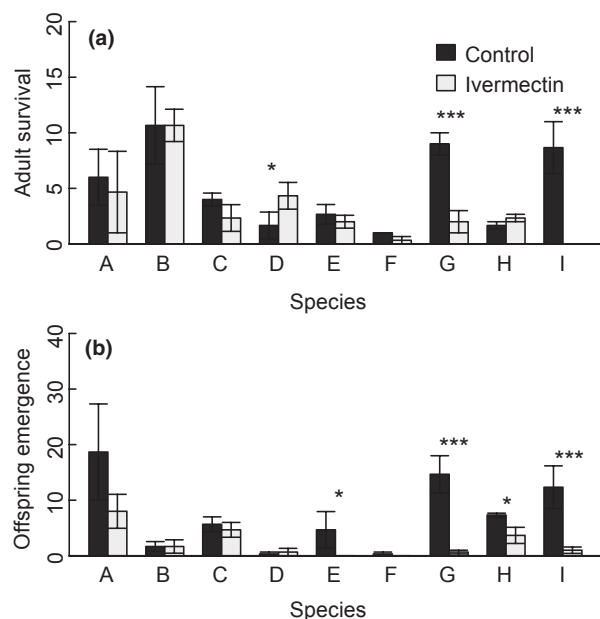


Fig. 2. Monoculture species-specific (a) adult survival and (b) offspring emergence in control and ivermectin dung. Bars are estimated means (and standard errors). Key to species codes: A = *Aphodius ater*, B = *Aphodius granarius*, C = *Aphodius pedellus*, (dung-ovipositing endocoprids), D = *Aphodius depressus*, E = *Aphodius fossor*, F = *Aphodius luridus*, (soil-ovipositing endocoprids), G = *Aphodius erraticus*, H = *Onthophagus joannae*, I = *Onthophagus similis* (paracoprids). Species-specific significant differences due to ivermectin are indicated as follows: * $P < 0.05$, *** $P < 0.001$.

for ecosystem service provision may be questioned. Furthermore, we collected dung at peak ivermectin dung concentration, so the results may be considered a 'worst-case scenario' when attempting to generalize to real agro-ecosystems.

FUNCTIONAL GROUP EFFECTS

Functional group identity was an important determinant of ecosystem functioning, as also documented by Slade *et al.* (2007) in a tropical forest dung beetle assemblage. We found disproportionate contributions of particular functional groups to dung decomposition: paracoprids outperformed dung- and soil-ovipositing endocoprids, although only in the short term. It is possible that hot, dry conditions during the first 4 weeks of the experiment primarily affected endocoprid species, which often use the dung pat for longer than paracoprids (Landin 1959, 1961). However, adult paracoprid beetles, by their action of physically burying dung matter, can cause a reduction in dung mass in the short term (Doube 1990), while endocoprid adult feeding activity on the liquid fraction would not have such a great effect on short-term mass loss. Endocoprid activity may in fact increase pat moisture (and mass) due to excretion during feeding (Landin 1961) and, in the case of soil-ovipositing endocoprids, cause soil to adhere to the base of pats (Owen *et al.* 2006). However, long-term positive effects of endocoprid activity on decomposition

include aeration (Holter 1979) and increased microbial biomass within the pat (Breymeyer, Jakubczyk & Olechowicz 1975; Lussenhop *et al.* 1980) due to adult and longer-term larval feeding, compared with short-term adult feeding only by paracoprids. This may explain long-term pat mass stabilization between functional groups and may be more representative of true pat organic matter loss. Such temporal differences suggest that many studies, which are typically carried out over relatively short durations, such as 28 (Barth *et al.* 1993), 63 (Barth *et al.* 1994) or 70 (Dimander, Hoglund & Waller 2003) days, may not fully and accurately document rates of dung decomposition.

IVERMECTIN EFFECTS

Lethal and sublethal impacts of ivermectin on dung beetles are well documented (reviewed recently by Wall & Beynon 2012). We found species-specific sensitivity to ivermectin for both adult beetles and their offspring. Contrary to expectation, *A. depressus* adult survival was significantly higher in ivermectin compared with control dung. We are unaware of previous examples of ivermectin apparently enhancing survival for any invertebrate species, and we recommend additional, better-replicated experiments with *A. depressus* to investigate this unexpected result.

Evidence for an associated functional effect of ivermectin on dung decomposition is less consistent (Wall & Strong 1987; Wratten *et al.* 1993; Barth *et al.* 1994). This discrepancy is likely to be due to a combination of factors, including the highly seasonal nature of north temperate dung decomposer communities, local variations in community species composition, weather effects on decomposition, and methodological problems due to confounding animal groups or pastures with treatment (Beynon *et al.* 2012).

Ivermectin treatment did not alter rates of dung decomposition when there were no dung beetles, suggesting that the ivermectin effects observed when dung beetles were present are due to ivermectin causing changes in the dung beetle communities and not due to ivermectin affecting other decomposition processes within the dung. There was also no significant ivermectin effect by the start of the following grazing season (at 36 weeks), suggesting the importance of long-term decomposition processes such as meso-faunal and microbial decomposition and abiotic weathering. From an applied perspective, efficient functionality within a whole grazing season is important in maximizing pasture yields (Bang *et al.* 2005), preventing rejection by livestock of herbage surrounding pats (MacLusky 1960) and preventing parasite spread (Gormally 1993).

WIDER IMPLICATIONS FOR MANAGEMENT OF AGRO-ECOSYSTEMS

Agricultural intensification is associated with reductions in biodiversity (Matson *et al.* 1997; Firbank *et al.* 2008; Perrings *et al.* 2010), which may also affect ecosystem ser-

vices important in agricultural output and sustainability (Bateman *et al.* 2010; Burkhard, Petrosillo & Costanza 2010; Balmford *et al.* 2011). Our results suggest that despite apparent species redundancy in an undisturbed system, maintaining species-rich assemblages in the face of changing environmental conditions ensures that ecosystem services are maintained. We therefore must be cautious in labelling species as 'redundant' when generalizing from less disturbed systems.

In an agricultural context, diversity and/or richness–ecosystem service relationships have been studied for pollination (e.g. Klein, Dewenter & Tscharntke 2003), crop yields (e.g., Hooper & Dukes 2004) and dung decomposition (e.g. Rosenlew & Roslin 2008; O'Hea, Kirwan & Finn 2010). However, studies of the impacts of livestock anthelmintics on dung fauna and functioning have generally been limited to field experiments (Wall & Strong 1987; Dimander, Hoglund & Waller 2003) or single-species laboratory toxicity studies (Hempel *et al.* 2006; Roembke *et al.* 2009). Field experiments often provide variable results (e.g. Svendsen *et al.* 2003), while simplified laboratory studies may give unrealistic predictions of effects at a field scale. Semi-field mesocosm experiments such as those described here have the potential to bridge this gap (Benton *et al.* 2007; Naeem 2008; Jochmann *et al.* 2011).

The complex effects of ivermectin on patterns of functioning revealed by our experiments suggest that it may be problematic to use toxicity data in combination with diversity-functioning theory to model the large-scale, area-wide functional consequences of anthelmintics. Instead, experimental data on anthelmintic effects on such patterns and processes should be used to drive models such as those suggested by Caron-Lormier *et al.* (2009, 2011) to predict large-scale, long-term impacts of anthelmintic effects on dung invertebrates and decomposition. A similar, multi-scale approach may also be needed to understand fully the consequences of management decisions for a variety of other ecosystem services in agro-ecosystems.

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Fig. S1. Layout of mesocosms at study site.

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