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Resources

Dung beetle assemblages, dung removal and secondary seed dispersal: data from a large-scale, multi-site experiment in the Western Palaearctic

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Abstract

By manipulating faeces during feeding and breeding, dung beetles (Coleoptera: Scarabaeidae) fulfil important ecosystem functions in terrestrial ecosystems throughout the world. In a pan-European multi-site experiment (MSE), we estimated the ecosystem functions of dung removal and secondary seed dispersal by differing combinations of dung beetle functional groups. Therefore, we classified dung beetles into five functional groups according to their body size and dung manipulation method: dwellers, large and small tunnelers, and large and small rollers. Furthermore, we set up a dung beetle sampling database containing all sampled dung beetles during the project. By identifying dung beetle specimens to the species level, we obtained a detailed insight into the dung beetle communities at each study location.

By establishing experimental plots allowing and inhibiting specific combinations of functional groups in the local dung beetle assemblage from removing dung and seeds, we estimated the role of each group in dung removal and secondary seed dispersal during a 4-week period. We performed all experiments in grazed (semi-) natural grasslands, and used different dung types (cattle, horse, sheep, goat or red deer) to match the herbivore species grazing in close vicinity of each of the study areas. Simultaneously, we sampled dung beetle assemblages by using pitfalls baited with the same dung types as used in the experiments.

This data paper documents two datasets collected in the framework of this MSE project. All the experiments took place between 2013 and 2016 at 17 study sites in 10 countries and 11 biogeographic zones. The entire *dung beetle sampling dataset* was published as a sampling event dataset at GBIF. The dataset includes the sampling results of all 17 study sites, which contain 1,050 sampling events and 4,362 occurrence records of 94 species. The second dataset contains the results of the dung removal and secondary seed dispersal experiments in which we used 11 experimental treatments and the five dung types mentioned above. This *experimental results dataset* holds all experimental results of the MSE project (11,537 records), and was published in the online data repository Zenodo.

Keywords: Dung beetles, ecosystem functioning, functional diversity, multi-site experiments

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This paper describes:

version 1.8 of the dung beetle sampling dataset at GBIF: https://www.gbif.org/dataset/bcbfd319-8813-4b6d-b529-07dc5a6ccf56, and

version 1.0 of the experimental results at Zenodo: https://zenodo.org/record/1115523

Introduction

The manipulation of faeces during the feeding and nesting process of dung beetles (Coleoptera: Scarabaeidae) brings about a series of ecosystem functions directly related to the removal of dung (Nichols et al. 2008). These functions include economically valuable ecosystem functions and services such as nutrient cycling (Sitters et al. 2014), the enhancement of soil hydrological properties through bioturbation (Brown et al. 2010), increased plant growth (Bang et al. 2005), and a reduced transmission of gastrointestinal parasites (Gregory et al. 2015). In addition to these ecosystem functions with a clear and direct economic return, dung beetles are of great relevance in plant dispersal ecology. Endozoochory, or the dispersal of plant seeds following ingestion, digestion, and defecation by herbivores, is commonly found in temperate grassland ecosystems (Mouissie et al. 2005). As dung beetles do not feed on seeds but rather bury seeds unintentionally with dung (Nichols et al. 2008), secondary seed dispersal can be considered an indirect result of dung beetle behaviour.

Dung beetles are rather diverse in terms of dung manipulation and nesting strategies, and they can be classified into three main functional groups: tunnelers (paracoprids) make vertical shafts beneath dung pats, rollers (telecoprids) transport dung in a combined horizontal and vertical movement by rolling a dung ball and burying it shallowly, and dwellers (endocoprids) reside in the original dung deposit (Doube 1990). As the functional composition of dung beetle assemblages highly depends on geography, habitat, elevation, and dung quality (Hanski, Cambefort 1991, Menéndez, Gutiérrez 1996), the ecosystem functions provided locally by dung beetles are closely linked with the local functional composition of dung beetle assemblages.

Due to their broad geographic distribution and presence in nearly all terrestrial habitats (Hanski, Cambefort 1991), dung beetles are a very suitable proxy for explaining general patterns in biodiversity and studying the link between biodiversity and ecosystem functions. Furthermore, scarabid beetles can be easily sampled within a wide range of sites using standardized protocols and, therefore, provide useful data for comparing levels of biodiversity across multiple spatial scales (Spector 2006). As most of the ecosystem functions provided by dung beetles are related to the local removal and underground burial of dung (Nichols et al. 2008), the effects of the manipulation of dung beetle diversity on ecosystem functioning can be studied at small spatial scales (Manning et al. 2016). However, despite the global distribution of Scarabaeidae species, most of the studies on the role of dung beetles in ecosystem function focus either on tropical and subtropical regions or are conducted in agricultural landscapes or microcosms. Studies on the impact of various dung beetle assemblages in semi-natural landscapes in the Western Palaearctic region are scarce. To fill this gap, we conducted a large-scaled field experiment at multiple sites in different biogeographic regions in the Western Palaearctic. In this pan-European multi-site experiment, we studied the link between ecosystem functions (dung removal and secondary seed dispersal) and dung beetle diversity and abundance. We selected grazed (semi-)natural grasslands throughout the Western Palaearctic zone.

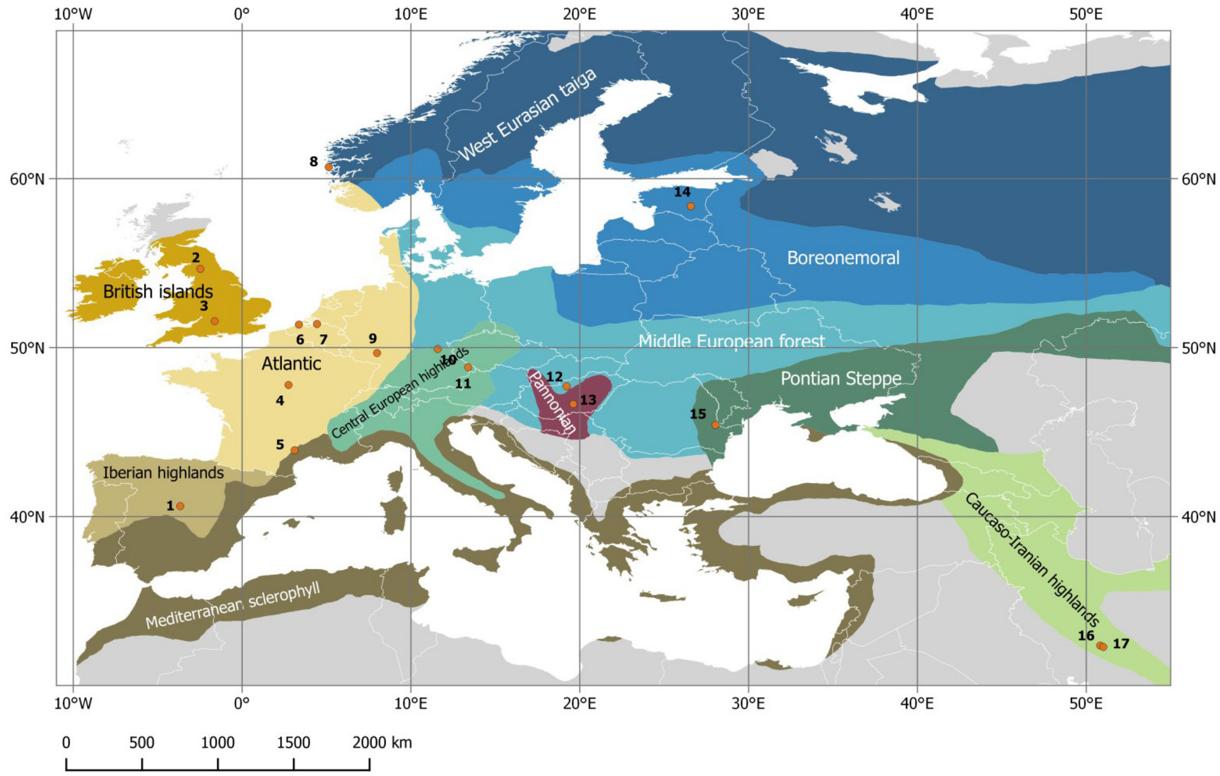


Figure 1. Dung beetle sampling locations in the ALTER-Net MSE III experiment, and their position within biogeographic provinces (as defined by Udvardy (1975); the digital base map was adapted from FAO Geonetwork (2015)). Names and exact locations of the study sites are given in Table 1.

By establishing experimental plots allowing and inhibiting specific combinations of functional groups in the local dung beetle assemblage from removing dung and seeds, we estimated the role of each group in dung removal and secondary seed dispersal.

During the experiment, we measured the removal of different types of dung and seeds, and we determined the dung beetle assemblage composition using different dung types as bait. The experiments took place between 2013 and 2016 at 17 study sites in 10 countries. In this data paper, we document the dung beetle dataset which contains all dung beetle specimens sampled during this project and the dataset resulting from the dung removal and secondary seed dispersal experiments.

Material and methods

Study sites

We carried out the multi-site experiment at 17 study sites in 10 countries in the Western Palaearctic realm, roughly covering an area of 25° to 70° latitude and -15° to 65° longitude (Figure 1). We assigned study sites to biogeographic regions (Udvardy 1975) and Köppen-Geiger climate zones (Peel et al. 2007). We replicated the experiment at a spatial scale by selecting study sites within the same biogeographic regions and/or climate zones (Table 1) and at a temporal scale by repeating the experiment in 2013, 2014, 2015, and/or 2016. We led all experiments and sampling during the main activity period of dung beetles in each region, which was during the summer for most study sites (Table 2). All study areas consisted of natural grasslands which had been grazed by domestic and/or wild herbivores for at least a couple of years prior to the experiment. At each study site, we fenced an experimental area of ca. 300 m² to prevent the interference of large herbivores with the experiments and dung beetle sampling, while the dung fauna associated with these large herbivores could enter the experimental zone without any restrictions.

In addition to their classification in biogeographic regions and climate zones, we defined EUNIS habitat types (as defined by the European Environmental Agency[1]) and soil types (according to soil texture analyses and the World Reference Base for Soil Resources, WRB; IUSS Working Group 2006) for each study area (Table 3). For each study site, we selected the nearest weather station from the monthly summary observations map of NOAA, which compiles worldwide weather data. We downloaded temperature data (lowest, mean minimum, mean, mean maximum, highest) and

1 www.eea.europa.eu, accessed May 2016

Table 1. Name, country and coordinates (latitude, longitude and elevation) of the study sites, and their classification in biogeographic regions (Udvardy 1975) and Köppen-Geiger climate zones (Peel et al. (2007), with BWk: cold desert climate, Cfb: warm summer maritime temperate climate, Cfc: cold summer maritime temperate climate, Csb: dry and warm summer Mediterranean climate, Dfa: hot summer continental climate, and Dfb: warm summer continental climate). Site codes match the numbers on the map in Figure 1.

Site code	Name	Country	Biogeographic region (Udvardy 1975)	Climate zone (Peel et al. 2007)	Latitude	Longitude	Elevation (m)
1	Castillo de Viñuelas	Spain	Iberian highlands	Csb	40° 36’ 49’’ N	03° 39’ 50’’ W	680
2	Moor House National Nature Reserve	UK	British islands	Cfb	54° 39’ 28’’ N	02° 37’ 29’’ W	446
3	Swindon	UK	British islands	Cfb	51° 33’ 54’’ N	01° 19’ 14’’ W	80
4	Le Chesnoy	France	Atlantic	Cfb	47° 47’ 07’’ N	02° 44’ 55’’ E	90
5	INRA, La Fage	France	Mediterranean sclerophyl	Csb	43° 55’ 31’’ N	03° 06’ 34’’ E	780
6	The Zwin	Belgium	Atlantic	Cfb	51° 21’ 45’’ N	03° 22’ 02’’ E	3
7	Kalmthout	Belgium	Atlantic	Cfb	51° 23’ 32’’ N	04° 26’ 05’’ E	18
8	Lyngheisenteret, Lygra	Norway	West Eurasian taiga	Cfc	60° 41’ 14’’ N	05° 07’ 44’’ E	20
9	Steinbühl	Germany	Atlantic	Cfb	49° 40’ 54’’ N	08° 00’ 02’’ E	320
10	Bayreuth	Germany	Central European highlands	Dfb	49° 55’ 02’’ N	11° 35’ 17’’ E	355
11	Bavarian Forest National Park	Germany	Central European highlands	Dfb	48° 49’ 58’’ N	13° 23’ 53’’ E	1150
12	Vácrátót	Hungary	Middle European forest	Dfa	47° 42’ 21’’ N	19° 13’ 47’’ E	176
13	Bugac	Hungary	Pannonian	Dfb	46° 39’ 23’’ N	19° 37’ 10’’ E	106
14	Tähtvere parish	Estonia	Boreonemoral	Dfb	58° 22’ 20’’ N	26° 35’ 01’’ E	67
15	Braila Islands	Romania	Pontian steppe	Dfa	45° 25’ 08’’ N	28° 02’ 47’’ E	2
16	Shahrekord	Iran	Caucaso-Iranian highlands	BWk	32° 21’ 43’’ N	50° 49’ 52’’ E	2055
17	Tange Sayad	Iran	Caucaso-Iranian highlands	BWk	32° 16’ 42’’ N	51° 01’ 17’’ E	2113

precipitation data (total monthly and extreme daily precipitation) for each study site and experimental period for statistical analyses[2].

Experimental design

We experimentally assessed dung removal and secondary seed dispersal of different combinations of dung beetle functional groups by constructing eleven exclosure types that had ground screens, vertical walls, and/or ceilings to prevent certain functional groups from removing dung (Figure 2). Each experimental unit had a square ground surface of 40 cm by 40 cm, and the walls were 15 cm high. The ground screens prevented tunnelers from removing dung , while walls prevented the dung removing activity of rollers. By combining walls and a ceiling, we prevented the

2 http://gis.ncdc.noaa. gov/maps, last accessed August 2016

Table 2. Number of experimental runs for dung removal and secondary seed dispersal experiments and the timing of the experiments in each study site. Secondary seed dispersal experiments were performed during experimental periods marked with asterisks (*), dung removal experiments were run during each experimental period and at each site.

Site code	Name	Experimental runs: dung removal	Experimental runs: secondary seed dispersal	Experimental period
1	Castillo de Viñuelas	1	-	June 2016
2	Moor House National Nature Reserve	2	1	mid June-mid July 2014*, July 2015
3	Swindon	1	-	mid June-mid July 2014
4	Le Chesnoy	2	1	June 2014*, June 2015
5	INRA, La Fage	1	-	May 2015
6	The Zwin	2	1	Aug 2014*, mid Sept-mid Oct 2014
7	Kalmthout	3	1	Aug 2014*, mid Sept-mid Oct 2014, mid Sept-mid Oct 2015
8	Lyngheisenteret, Lygra	1	-	Aug 2014
9	Steinbühl	2	1	June 2014*, June 2015
10	Bayreuth	2	-	June 2014, July 2015
11	Bavarian Forest National Park	2	1	Aug 2014*, July 2015
12	Vácrátót	2	-	June 2015, mid Sept-mid Oct 2015
13	Bugac	3	-	June 2014, June 2015, mid Sept-mid Oct 2015
14	Tähtvere parish	2	1	June 2014*, mid June-mid July 2015
15	Braila Islands	1	1	July 2014*
16	Shahrekord	6	6	Sept 2013*, Oct 2013*, mid Nov-mid Dec 2014*, June 2015*, September 2015*, October 2015*
17	Tange Sayad	6	6	Aug 2013*, Nov 2013*, mid Nov-mid Dec 2014*, June 2015*, September 2015*, October 2015*

Table 3. EUNIS habitat and soil type of each study site and the used dung types during the experiments and nearby grazer species.

Site code	Study site	EUNIS habitat type[1]	Soil type[2]	Dung type count	Used dung types	Nearby grazer species
1	Castillo de Viñuelas	Mediterranean montane grassland	vertic luvisol	1	cattle	cattle
2	Moor House NNR	Montane grassland	humic gleysol	2	cattle, sheep	sheep
3	Swindon	Semi-improved grassland/ agricultural land	eutric cambisol	1	cattle	cattle, sheep
4	Le Chesnoy	Grasslands	gleyic luvisol	3	cattle, sheep, red deer	cattle, horse, sheep, red deer
5	INRA, La Fage	Mediterranean montane grassland	eutric cambisol	1	sheep	sheep
6	The Zwin	Permanent mesotrophic pastures and aftermath-grazed meadows	calcaric fluvisol	3	cattle, horse, sheep	cattle, horse, sheep
7	Kalmthout	Temperate shrub heathland	humic podzol	3	cattle, horse, sheep	cattle, horse, sheep
8	Lygra	Grasslands	orthic podzol	3	cattle, horse, sheep	sheep
9	Steinbühl	Permanent mesotrophic pastures on former arable land	dystric cambisol	2	cattle, horse	cattle, horse
10	Bayreuth	Permanent mesotrophic pastures and aftermath-grazed meadows	stagnic gleysol	3	cattle, horse, sheep	cattle, horse, sheep
11	Bavarian Forest NP	Permanent mesotrophic pastures and aftermath-grazed meadows	dystric cambisol	2	cattle, horse	cattle, horse, red deer
12	Vácrátót	Grasslands	chromic cambisol	3	cattle, horse, sheep	cattle, horse, sheep
13	Bugac	Grasslands	calcaric regosol	3	cattle, horse, sheep	cattle, horse, sheep
14	Tähtvere parish	Permanent mesotrophic pastures and aftermath-grazed meadows	eutric podzoluvisol	2	cattle, sheep	cattle, sheep
15	Braila Islands	Grasslands	calcaric fluvisol	3	cattle, horse, sheep	cattle, horse, sheep
16	Shahrekord	Perennial calcareous grassland and basic steppes*	calcic xerosol	3	cattle, sheep, goat	cattle, sheep
17	Tange Sayad	Perennial calcareous grassland and basic steppes*	calcic xerosol	3	cattle, sheep, goat	cattle, sheep

[1] as defined in the European nature information system (EUNIS) by the European Environmental Agency (EEA, http://eunis.eea.europa.eu/). [2] as defined in the World Reference Base for Soil Resources (WRB) (IUSS Working Group 2006). * EUNIS habitat type was identified using the definitions of the types by the EEA in case study areas fall outside the borders of the pan-European classification.

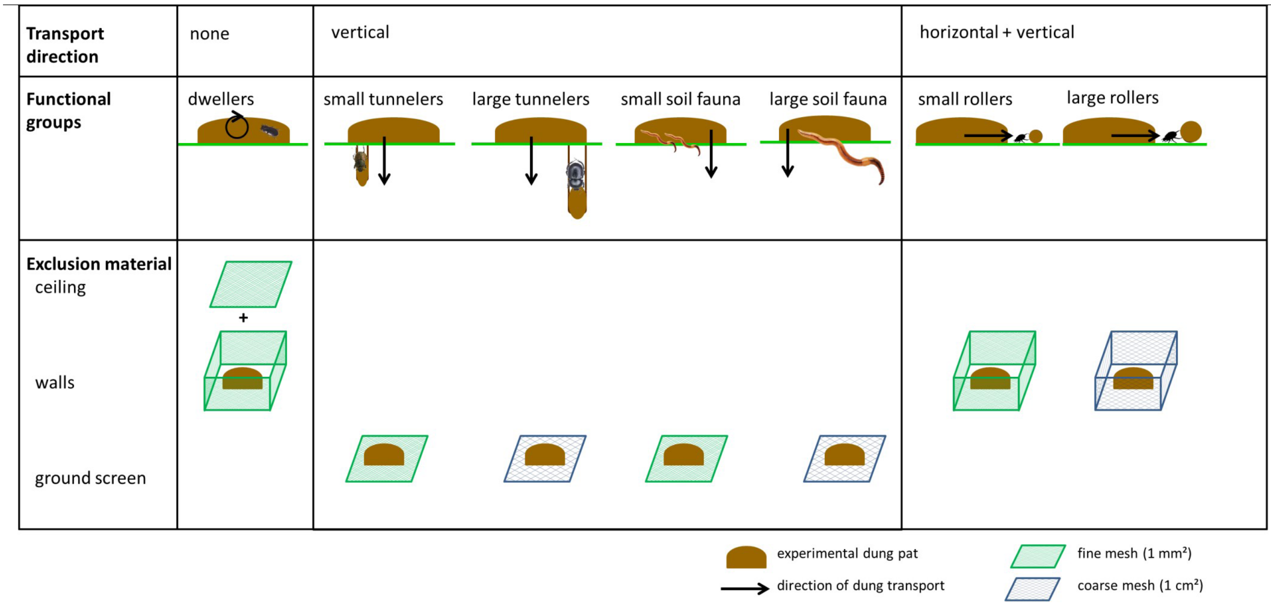


Figure 2. Functional groups defined in the experiments, the direction of dung transport for each group, and the type of material used to prevent dung removal by each functional group.

activity of all dung beetle functional groups. Ground screens, walls, and ceilings were made of plastic mesh; the large mesh size (square mesh with side lengths of 1 cm) prevented dung removal by large beetles (while including dung removal by smaller beetles able to move through 1 cm² holes), and the small mesh size (square mesh with side lengths of 1 mm) prevented all sizes of beetles in the relevant functional group from removing dung. As soil macro-invertebrates besides dung beetles also had access to our experimental dung piles, we also monitored dung removal by this non-identified group of organisms. Consequently, we measured dung removal and secondary seed dispersal of seven functional groups based on dung removal behaviour and body size: dwellers, small and large tunnelers, small and large rollers, and small and large soil macro-invertebrates aside from dung beetles (Table 4).

We measured dung removal by putting known quantities of dung in the experimental plots and weighing the amount of dung remaining after one month. Similarly, we assessed secondary seed dispersal by putting known quantities of seeds in standardized dung pats and counting the seeds left after one month. We used three different seed types: elongated and large-sized seeds (6 mm, caryopses of *Alopecurus myosuroides*), spherical and medium-sized seeds (3 mm, mericarps of *Galium aparine*), and elongated in small-sized seeds (1 mm, caryopses of *Poa annua*). We purchased all seeds in a specialized web shop (www.herbiseed.com). To avoid seed loss caused by germination during the experiment, seeds were, prior to the experiment, sterilized by dry heating at 80 °C for 7 days. As, after 60 days, no seedlings emerged in the subsequent germinability test on 1 % water agar in laboratory conditions, we assumed that no germination would occur during the field experiment. We spray-painted each seed species in distinct fluorescent colours to increase visibility, and mixed ten seeds of each species with the homogenized dung portions. We used cattle dung as a reference dung type at all study sites (except site 5), and at most sites, we replicated the experiment using the dung of herbivores living in or nearby the study area (including horse, sheep, red deer, and goat dung; see Table 3 for a complete list). In study areas with no previous records of roller species, we did not install treatments focussing specifically on rollers (Table 4). We replicated each experimental unit six times for each dung type, and we grouped units using the same dung type in blocks. Within each block, experimental units were set up in a fully randomized design. Individual experimental units were 60 cm apart, while different blocks were at least 2 m apart (Figure 3).

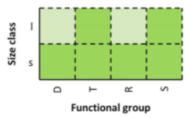
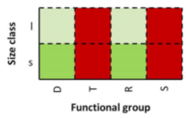
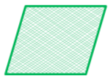
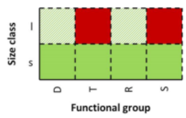
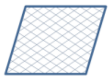
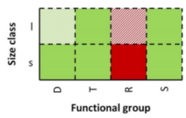
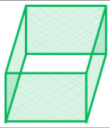
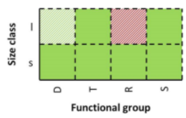
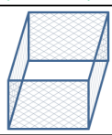
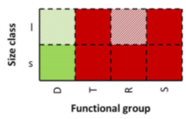
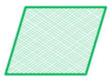
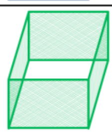
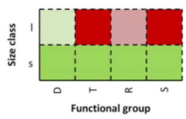
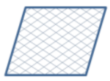
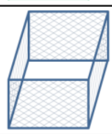
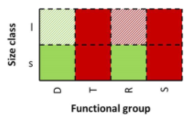
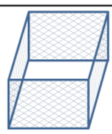
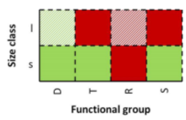
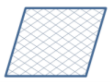
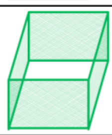
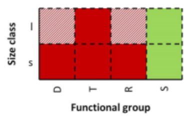
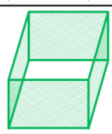
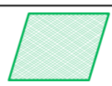
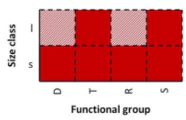
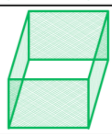
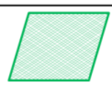
At the start of the experiment, we took fresh subsamples of each dung batch and weighed them to use as a reference sample. Subsequently, we oven-dried reference samples (80°C) and measured the dry weight. At the end of the experiment, we collected the remaining dung in the experimental units, oven-dried it, and again measured the dry mass.

We calculated *Dung Removal Ratio (DRR)* using formula 1:

$$\mathrm{DRR} = \frac{\mathrm{M_{initial}} - \mathrm{M_{final}}}{\mathrm{M_{initial}}} \quad \text{(formula 1)}$$

where $M_{initial}$ is the average dry mass of the reference samples and M_{final} is the dry mass of the remaining dung at the end of the experiment.

Table 4. Treatments used in the dung and seed removal experiments and the functional groups (with D= dwellers, T= tunnelers, R= rollers, and S= soil macro-invertebrates) and size classes (with l= large and s= small body size) able to move dung in each treatment. Green boxes indicate the inclusion of a functional group; red boxes mark excluded groups. Large dweller or roller species were not found (dashed boxes). Materials used for ground screens, walls and ceilings were either fine mesh (green, 1 mm²), or coarse mesh (blue, 1 cm²). Exclosure types marked with an asterisk (*) were not built at study sites where no rolling species occur (Bavarian Forest NP, Castillo de Viñuelas, Le Chesnoy, Lygra, Moor House NP, Steinbühl, Tähtvere parish, Vácrátót and Swindon in all experimental runs, and in Bugac, Bayreuth and Kalmthout during the experiments in 2015). In the control treatment (t11), dung degradation was measured in the absence of invertebrates unable to move through 1 mm² mesh.

treatment code	functional groups	groundscreen	wall	ceiling
t01				
t02				
t03				
t04*				
t05*				
t06*				
t07*				
t08*				
t09*				
t10				
t11				

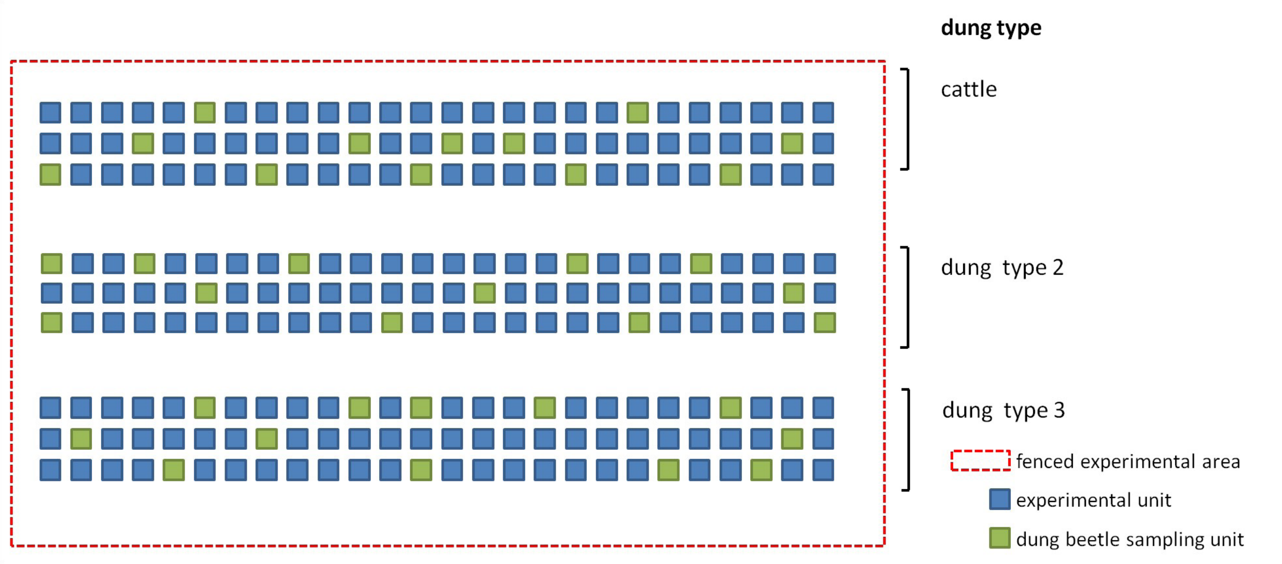


Figure 3. Experimental design with the random distribution of experimental units and dung beetle sampling units grouped by dung types in the fenced experimental area.

Similarly, we calculated secondary *Seed Dispersal Ratio (SDR)* for each seed size class (small, medium and large sized seeds) with formula 2:

$$\mathrm{SDR} = \frac{S_{\mathrm{initial}} - S_{\mathrm{final}}}{S_{\mathrm{initial}}} \qquad \text{(formula 2)}$$

where $S_{initial}$ is the number of seeds put in the dung samples, and S_{final} is the number of seeds retrieved from the samples at the end of the experiment.

Therefore, both DRR and SDR range between 0 and 1.

Dung beetle sampling methods

We sampled the dung beetle community in each study area during the dung removal and secondary seed dispersal experiments. In 2013 and 2014, we used two types of pitfall traps to achieve a complete view of dung beetle diversity and abundance. The first trap type consisted of one large container (1 l) with an 11 cm wide opening at the top ("T1" traps, Figure 4). To prevent by-catch of vertebrates, T1 traps were covered with hexagonal chicken wire (with a mesh diameter of 25 mm). We attached approximately 100 g of dung, packed in a nylon bag, to the chicken wire to attract dung fauna (as in Larsen, Forsyth (2005)). The second trap type consisted of five smaller containers (0.2 l) with a 7 cm wide opening at the top surrounded by a central dung pile of approximately 300 g ("T5" traps as used by D'hondt et al. (2008), Figure 4). As the dung beetle species richness did not differ between trap types in the first two years, the sampling effort was lowered in the 2015 and 2016 experiments by using a

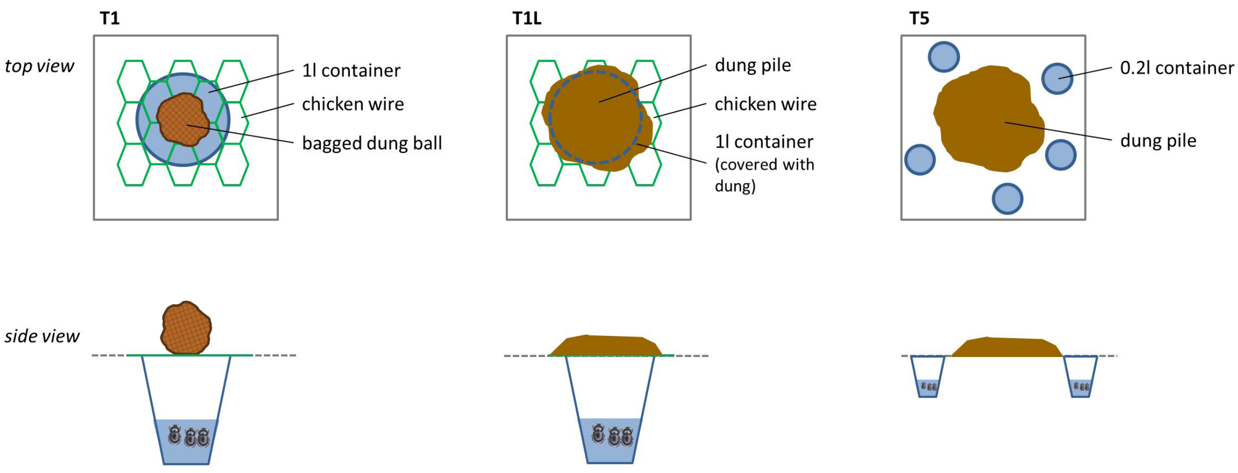


Figure 4. Schemes of the used trap types: 1 large pitfall covered with a dung ball in a nylon bag (T1, left), 1 large pitfall covered with a large, unpacked dung pile (T1L, middle), and 5 small pitfalls surrounding a central dung pile (T5, right). For each of the trap types a top view and a side view is provided.

variant of the T1 pitfall traps; these were baited with 500 g of unwrapped dung instead of smaller portions of wrapped dung (“T1L” traps in Figure 4). In all trap types, we dug containers into the soil with the upper rim levelled with the soil surface. We filled containers with a saturated salt-water solution (ca. 365 g l^{-1} NaCl with some drops of unscented detergent) and we baited them with the same dung types as used in the dung removal experiments (Table 3). We set up both trap types randomly between the experimental units with six replicates per dung and trap type (Figure 3). We put the traps in operation one week after the start of the dung removal and secondary seed dispersal experiments to avoid interference with the initial beetle colonization phase of the experiment. We emptied traps weekly over a three-week period. To relate dung beetle abundance and richness with dung quality, we reused the original dung baits after emptying the pitfalls. We extracted dung beetle specimens from the samples and identified to species level. For each species, we counted the number of individuals per sampling unit (pitfall) with indication of sampling date, dung bait used, and geographic location.

Taxonomic coverage and dung beetle classification

We defined ‘dung beetles’ as species of the superfamily Scarabaeoidea that generally feed on dung in both the larval and adult phase. Some species of other beetle families such as Hydrophilidae and Staphylinidae are also commonly found in dung and could be considered dung beetles as well (Hanski, Cambefort 1991). Nevertheless, they are not coprophagous during their entire life cycle (Finn et al. 1999), and they do not contribute to lateral or vertical dung transport which was one of the major research goals of our study. Therefore, dung beetles were strictly defined as the coprophagous species in the Geotrupidae and Scarabaeidae families.

In a further step, we classified dung beetle species in three functional groups according to the species’ dung processing behaviour: putting dung in vertical shafts dug underneath dung pats (paracoprids or tunnelers), rolling dung balls in a horizontal direction (telocoprids or rollers), or feeding and nesting in the dung pat itself (endocoprids or dwellers). Following Hanski, Cambefort (1991), we classified all Geotrupidae species, the Scarabaeinae species of the genera *Caccobius*, *Copris*, *Euoniticellus*, *Euonthophagus*, *Onitis,* and *Onthophagus;* and one Aphodiinae species (*Colobopterus erraticus*, see Rojewski (1983)) as tunnelers. We classified the remaining Scarabaeinae species (genera: *Gymnopleurus*, *Sisyphus*) in our dataset as rollers, while dwellers comprised all Aphodiinae species, except for *Colobopterus erraticus,* which is a tunneling Aphodiinae species.

Datasets

Dung beetle sampling dataset

- **Object name**: Dung beetles in the Western Palaearctic
- **Format name**: Darwin Core Archive format
- **Format version**: 1.8
- **Character encoding**: UTF-8
- **Language**: English
- **License**: http://creativecommons.org/publicdomain/zero/1.0/
- **Usage norms**: http://www.inbo.be/en/norms-for-data-use
- **Publication date**: First publication date 2017-08-21
- **Distribution**: https://ipt.inbo.be/resource?r=dbwp-events
- **DOI**: https://doi.org/10.15468/zbazdy

We set up the dung beetle sampling dataset as a sampling event database in the Darwin Core Archive format used by the Global Biodiversity Information Facility (GBIF). It consists of two datasets: an ‘event’ dataset containing information on 1,050 sampling events and an ‘occurrence’ dataset holding 4,362 records of dung beetle species. We defined each sampling event as a unique event whenever a specific sampling unit baited with a specific dung type and located at a specific study site was emptied. In case sampling pots were empty, lost, or destroyed during the sampling period, those events were not included in the dataset. For example, an experiment ran once at a particular study area using 2 sampling methods and one type of dung led to 36 sampling events (1 study site x 1 experimental run x 2 sampling methods x 1 dung type x 3 sampling weeks x 6 replicates). More specifically, the event dataset contains detailed information on the sampling protocol (types of sampling units and dung baits used), event date, habitat, continent, country, locality, elevation, latitude and longitude. In total, we recorded 1,050 sampling events using cattle (478), horse (209), sheep (330), goat (3), and red deer dung (30) at 17 study sites (Figure 5). The occurrence dataset contains 4,362 observations of 94 species (Figure 6). Both the species diversity and the number of specimens sampled were highly variable between sites (Figure 7 and Figure 8). This dataset contains information on the local dung beetle community of specific sites that were included in our field experiment. For some of these sites, dung beetle communities and species richness are not very well known yet, so our dataset can contribute to this knowledge. We should, however, note that our sampling campaign was limited to 17 study sites and was only done in specific seasons, so the dung beetle species list is most likely not complete for these sites.

Experimental results dataset

- **Object name**: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic [Dataset] (DungSeedRemoval.txt, StudySites.txt, Treatments.txt)
- **Format name**: txt
- **Format version**: 1.0
- **Character encoding**: UTF-8
- **Language**: English
- **License**: http://creativecommons.org/publicdomain/zero/1.0/

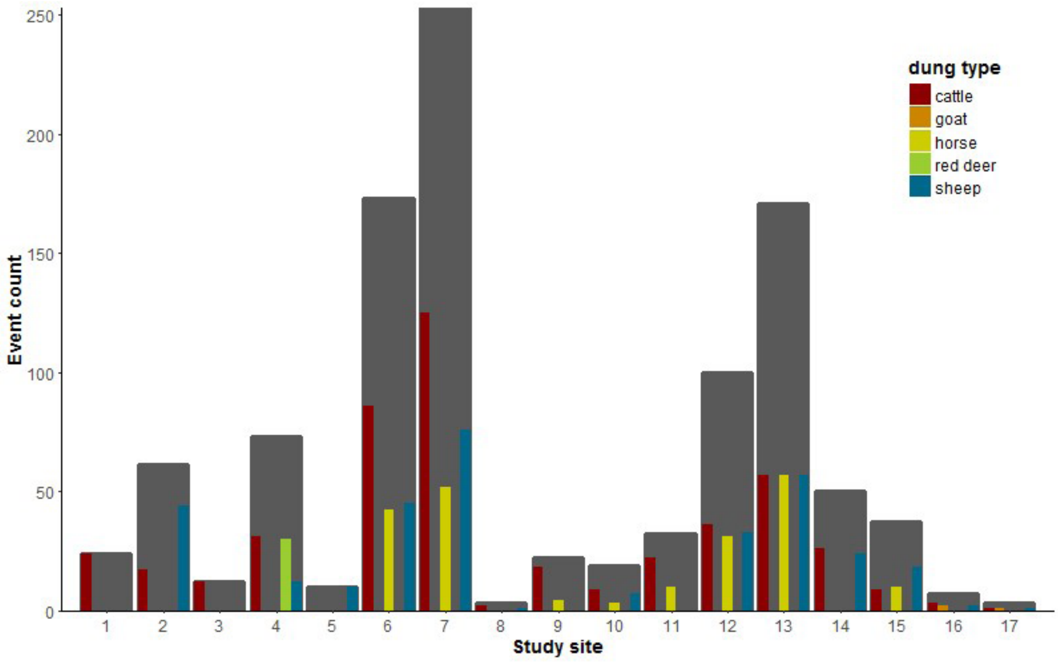


Figure 5. Total number of sampling events of dung beetles by study site (grey bars) and by dung type (coloured bars). Study site codes correspond with the codes in the map of Figure 1.

- **Usage norms**: http://www.inbo.be/en/norms-for-data-use
- **Publication date**: 13/12/2017
- **Distribution**: https://zenodo.org/record/1115523
- **DOI:** https://doi.org/10.5281/zenodo.1115523

We published the experimental results dataset as open data in the Zenodo repository. The directory consists of three separate files containing the experimental results (which is the core dataset, DungSeedRemoval.txt), metadata of the study sites (StudySites.txt), and metadata of the experimental treatments (Treatments.txt). The core dataset contains 11,537 records of dung removal and secondary seed dispersal results; it mentions study site codes, dung types, experimental treatment codes, timing of the experiment (month and year), and the duration of the experiment in days. We calculated dung removal and secondary seed dispersal ratios of small, medium, and large seeds using formulas 1 and 2, and we coded them as DRR, SDRsmall, SDRmedium, and SDRlarge respectively in the 'parameter' field. Study site codes are identical to those used in the GBIF dataset. We also provided site names, countries, and coordinates (latitude, longitude and elevation) as a text file in the Zenodo repository. We coded the eleven experimental treatments as t01, t02, ..., t11 as in Table 4. We also put the same information on Zenodo as a summarizing metadata text file indicating which of the six functional groups (dwellers, small tunnelers, large tunnelers, small rollers, large rollers, and other soil macro-invertebrates) could access the experimental dung pile in each treatment.

This dataset was used to answer key ecological questions on the effect different combinations of dung beetle functional groups have on ecosystem functions such as dung removal and secondary seed dispersal. An identical experimental set-up was used at all study sites, but the number of dung types used to replicate the experiment differed between sites. In all sites except La Fage, cattle dung was used, which enables the comparison of the removal of cattle dung between all study sites. The secondary seed dispersal experiment was done on a subset of sites (see table 2).

Usage norms

We have released the data to the public domain under a Creative Commons Zero waiver[3]. However, we would appreciate it if users read and followed these norms for data use[4], and referenced the original datasets links[5] whenever possible. If you use these data for a scientific paper, please cite the dataset following the applicable citation norms, and please consider us for co-authorship. We are always interested in knowing how the data has been used or in providing more information, so please contact us[6].

3 http://creativecommons.org/publicdomain/zero/1.0/

4 http://www.inbo.be/en/norms-for-data-use

5 https://doi.org/10.15468/zbazdy and https://doi. g/10.5281/zenodo.1115523

6 via the contact information provided in the metadata, opendata@inbo.be or at https://twitter.com/LifeWatchINBO.1

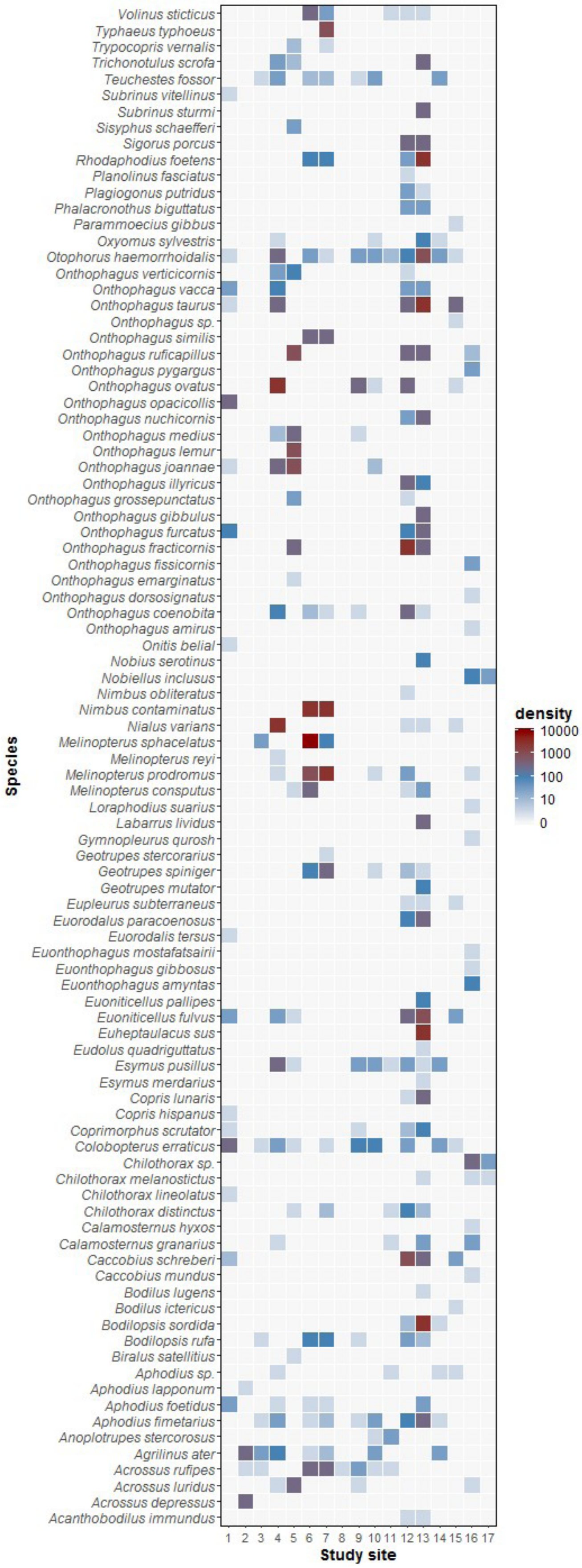


Figure 6. Heat plot of the species found in each study site. Colours indicate the total number of specimens collected of each species (density). Codes of study sites correspond with those in the map of Figure 1.

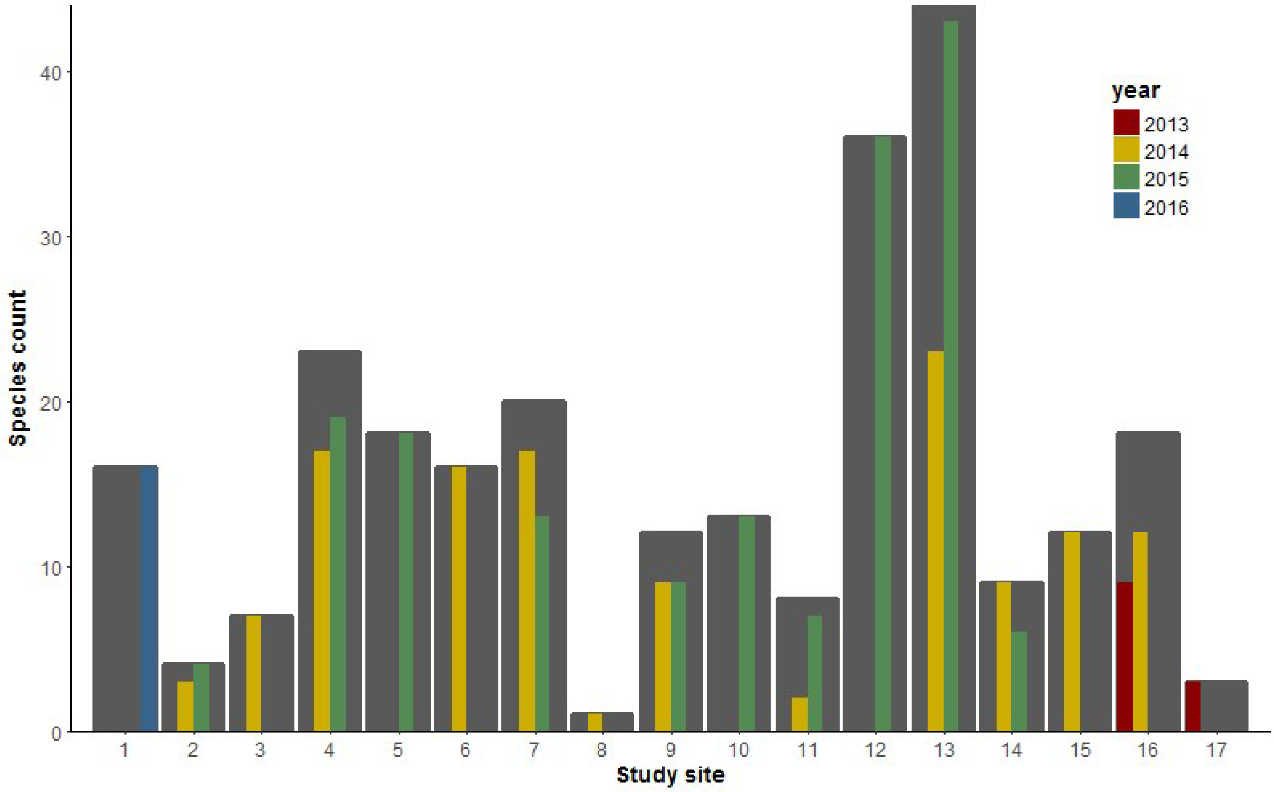


Figure 7. Total number of species collected in each study site (grey bars) and by sampling year (coloured bars). Study site codes correspond with those in the map of Figure 1.

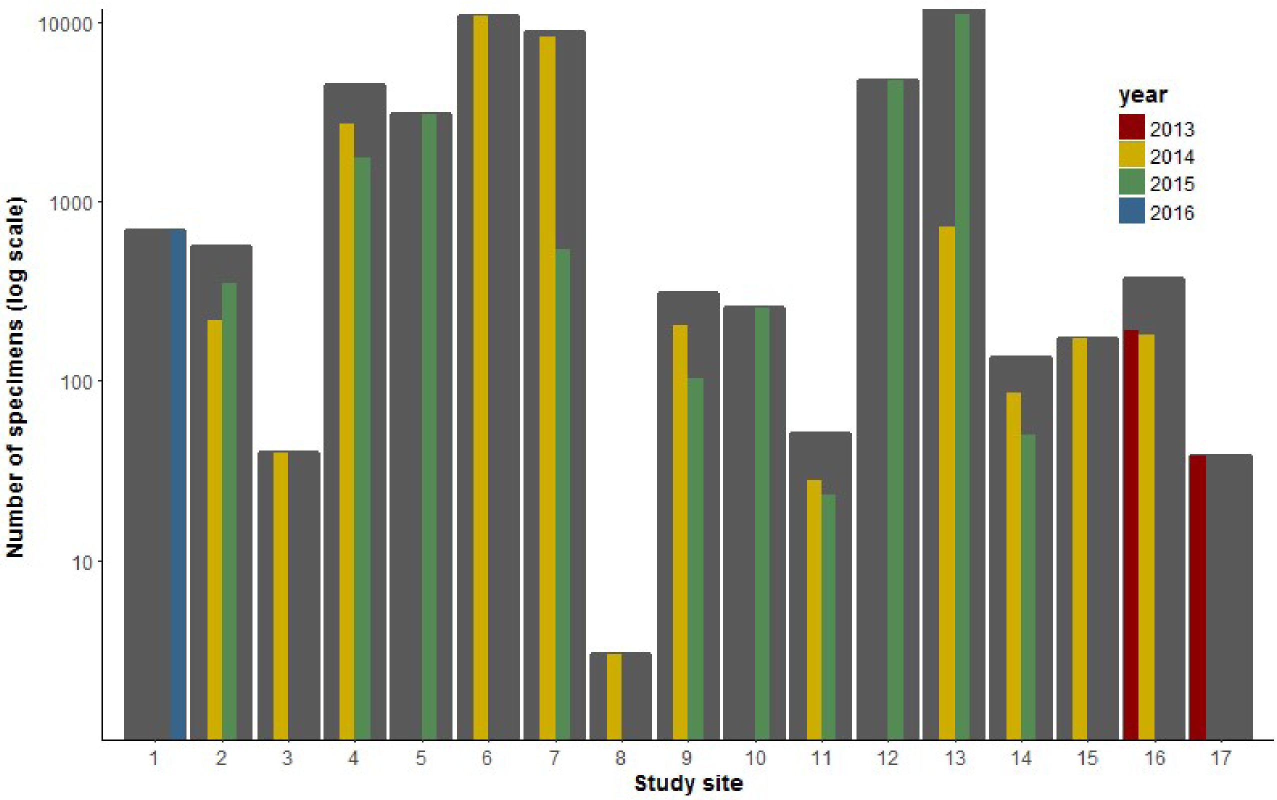


Figure 8. Total number of specimens in the dataset by study site (grey bars) and by sampling year (coloured bars). Study site codes correspond with those in the map of Figure 1.

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References

Bang, H.S., Lee, J.H., Kwon, O.S., Na, Y.E., Jang, Y.S. & Kim, W.H. (2005) Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Applied Soil Ecology, 29, 165-171.

Brown, J., Scholtz, C.H., Janeau, J.-L., Grellier, S. & Podwojewski, P. (2010) Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. Applied Soil Ecology, 46, 9-16.

D'hondt, B., Bossuyt, B., Hoffmann, M. & Bonte, D. (2008) Dung beetles as secondary seed dispersers in a temperate grassland. Basic and Applied Ecology, 9, 542-549.

Doube, B.M. (1990) A functional classification for analysis of the structure of dung beetle assemblages. Ecological Entomology, 15, 371-383.

FAO Geonetwork (2015). Udvardy's Ecoregions (GeoLayer). (Latest update: 04 Jun 2015) Accessed (9 Sep 2016). Url: http://data.fao.org/ref/beac5780-88fd-11da-a88f-000d939bc5d8.html?version=1.0.

Finn, J.A., Gittings, T. & Giller, P.S. (1999) Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland. Ecological Entomology, 24, 24-36.

Gregory, N., Gómez, A., Oliveira, T.M. & Nichols, E. (2015) Big dung beetles dig deeper: trait-based consequences for faecal parasite transmission. International Journal for Parasitology, 45, 101-105.

Hanski, I. & Cambefort, Y. (1991) Dung beetle ecology. Princeton University Press. Princeton, New Jersey, USA.

IUSS Working Group (2006) World reference base for soil resources 2006: A framework for international classification, correlation and communication. Food and Agriculture Organization of the United Nations. Rome, Italy.

Larsen, T.H. & Forsyth, A. (2005) Trap spacing and transect design for dung beetle biodiversity studies. Biotropica, 37, 322-325.

Manning, P., Slade, E.M., Beynon, S.A. & Lewis, O.T. (2016) Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. Agriculture, Ecosystems and Environment, 218, 87-94.

Menéndez, R. & Gutiérrez, D. (1996) Altitudinal effects on habitat selection of dung beetles (Scarabaeoidea: Aphodiidae) in the northern Iberian peninsula. Ecography, 19, 313-317.

Mouissie, A.M., Vos, P., Verhagen, H.M.C. & Bakker, J.P. (2005) Endozoochory by free-ranging, large herbivores: Ecological correlates and perspectives for restoration. Basic and Applied Ecology, 6, 547-558.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E. & TSRN (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation, 141, 1461-1474.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences Discussions Discussions, 4, 439-473.

Rojewski, C. (1983) Observations on the nesting behaviour of *Aphodius erraticus* L. (Coleoptera, Scarabaeidae). Bulletin Entomologique de Pologne, 53, 271-279.

Sitters, J., Maechler, M.J., Edwards, P.J., Suter, W. & Olde Venterink, H. (2014) Interactions between C: N: P stoichiometry and soil macrofauna control dung decomposition of savanna herbivores. Functional Ecology, 28, 776-786.

Spector, S. (2006) Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): An invertebrate focal taxon for biodiversity research and conservation. The Coleopterists Bulletin, 5, 71-83.

Udvardy, M.D.F. (1975) A classification of the biogeographical provinces of the world. IUCN Occasional paper 18, World Conservation Union. Morges, Switserland.

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