

# Functionally complete communities result in better ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic

---

Authors: Tanja Milotić, Christophe Baltzinger, Carsten Eichberg, Amy E. Eycott, Marco Heurich, Jörg Müller, Jorge A. Noriega, Rosa Menendez, Jutta Stadler, Réka Ádám, Tessa Bargmann, Isabelle Bilger, Jörn Buse, Joaquin Calatayud, Constantin Ciubuc, Gergely Boros, Pierre Jay-Robert, Märt Kruus, Enno Merivee, Geoffrey Miessen, Anne Must, Elham Ardali, Elena Preda, Iraj Rahimi, Dirk Rohwedder, Rob Rose, Eleanor M. Slade, László Somay, Pejman Tahmasebi, Stefano Ziani and Maurice Hoffmann

Handling editor: Christine Meynard

## Title page

### Title

Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic

### Authors

1. Tanja Milotić
2. Christophe Baltzinger
3. Carsten Eichberg
4. Amy E. Eycott
5. Marco Heurich
6. Jörg Müller
7. Jorge A. Noriega
8. Rosa Menendez
9. Jutta Stadler
10. Réka Ádám
11. Tessa Bargmann
12. Isabelle Bilger
13. Jörn Buse
14. Joaquín Calatayud
15. Constantin Ciubuc
16. Gergely Boros
17. Pierre Jay-Robert
18. Märt Kruus
19. Enno Merivee
20. Geoffrey Miessen
21. Anne Must
22. Elham Ardali
23. Elena Preda
24. Iraj Rahimi
25. Dirk Rohwedder
26. Rob Rose
27. Eleanor M. Slade
28. László Somay
29. Pejman Tahmasebi
30. Stefano Ziani
31. Maurice Hoffmann

### Postal addresses and email addresses of all authors

1. TM: Ghent University, Department of Biology, TERC, K.L. Ledeganckstraat 35, 9000 Gent, Belgium; Research Institute for Nature and Forest, Havenlaan 88/73, 1000 Brussels, Belgium ([tanja.milotic@inbo.be](mailto:tanja.milotic@inbo.be))
2. CB: Irstea, Domaine des Barres, 45290 Nogent-sur-Vernisson, France ([christophe.baltzinger@irstea.fr](mailto:christophe.baltzinger@irstea.fr)); Centre for Invasion Biology, School of Life Sciences, University of KwaZulu-Natal, Scottsville, 3209, Pietermaritzburg, South Africa

3. CE: University of Trier, Regional and Environmental Sciences, Geobotany, Behringstr. 21, 54296 Trier, Germany ([eichberg@uni-trier.de](mailto:eichberg@uni-trier.de))
4. AE: University of Bergen, Department of Biology, PO box 7803, 5020 Bergen, Norway ([amy.eycott@uib.no](mailto:amy.eycott@uib.no))
5. MH: Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany; University of Freiburg, Faculty of Environment and Natural Resources, Tennenbacher Str. 4, 79106 Freiburg, Germany ([marco.heurich@npv-bw.bayern.de](mailto:marco.heurich@npv-bw.bayern.de))
6. JM: Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany; University of Würzburg, Biozentrum, Glashüttenstraße 5, 96181 Rauhenebrach, Germany ([joerg.mueller@npv-bw.bayern.de](mailto:joerg.mueller@npv-bw.bayern.de))
7. JAN: National Museum of Natural Science (CSIC), Department of Biogeography and Global Change, C/José Gutiérrez Abascal 2, 28006 Madrid, Spain ([jnorieg@hotmail.com](mailto:jnorieg@hotmail.com))
8. RM: Lancaster University, Lancaster Environment Centre, Lancaster LA1 4YQ, UK ([r.menendez@lancaster.ac.uk](mailto:r.menendez@lancaster.ac.uk))
9. JS: Helmholtz Centre for Environmental Research - UFZ, Dept. Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle/Saale, Germany ([jutta.stadler@ufz.de](mailto:jutta.stadler@ufz.de))
10. RA: MTA Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4., H-2163 Vácrátót, Hungary; Eötvös Loránd University, Department of Plant Systematics, Ecology and Theoretical Botany, Pázmány Péter sétány 1/A, H-1117 Budapest, Hungary ([helleborus42@gmail.com](mailto:helleborus42@gmail.com))
11. TB: University of Bergen, Department of Biology, PO box 7803, 5020 Bergen, Norway; University of Bergen, Department of Geography, PO box 7802, 5020 Bergen, Norway, ([tessa.bargmann@uib.no](mailto:tessa.bargmann@uib.no))
12. IB: Irstea, Domaine des Barres, 45290 Nogent-sur-Vernisson, France ([isabelle.bilger@irstea.fr](mailto:isabelle.bilger@irstea.fr))
13. JB: University of Koblenz-Landau, Institute for Environmental Sciences, Ecosystem Analysis, Fortstr. 7, 76829 Landau, Germany; Black Forest National Park, Kniebisstr. 67, 72250 Freudenstadt, Germany ([joern.buse@nlp.bwl.de](mailto:joern.buse@nlp.bwl.de))
14. JC: Integrated Science Lab, Department of Physics, Umeå University, Umeå, Sweden ([j.calatayud.ortega@gmail.com](mailto:j.calatayud.ortega@gmail.com))
15. CC: University of Bucharest, Research Centre in Systems Ecology and Sustainability, Splaiul Independentei 91-95, 050095 Bucharest, Romania ([ciubuc1206@gmail.com](mailto:ciubuc1206@gmail.com))
16. GB: MTA Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4., H-2163 Vácrátót, Hungary; MTA Centre for Ecological Research, GINOP Sustainable Ecosystem Research Group, Klebelsberg u. 3., H-8237 Tihany, Hungary; Szent István University, Department of Zoology and Animal Ecology, Páter Károly u. 1., H-2100 Gödöllő, Hungary ([boros.gergo@okologia.mta.hu](mailto:boros.gergo@okologia.mta.hu))
17. PJR: CEFÉ, Univ. Paul Valéry Montpellier 3, Univ. Montpellier, EPHE, CNRS, IRD, Montpellier, France ([pierre.jay-robert@univ-montp3.fr](mailto:pierre.jay-robert@univ-montp3.fr))
18. MK: Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Kreutzwaldi Street 1, 51014, Tartu, Estonia ([mart.kruus@emu.ee](mailto:mart.kruus@emu.ee))
19. EM: Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Kreutzwaldi Street 1, 51014, Tartu, Estonia ([enno.merivee@emu.ee](mailto:enno.merivee@emu.ee))
20. GM: independent researcher, Liège, Belgium, ([geoffrey.miessen@skynet.be](mailto:geoffrey.miessen@skynet.be))
21. AM: Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Kreutzwaldi Street 1, 51014, Tartu, Estonia ([anne.must@emu.ee](mailto:anne.must@emu.ee))
22. EA: Ghent University, Department of Biology, K.L. Ledeganckstraat 35, 9000 Gent, Belgium; Shahrekord University, Department of Rangeland and Watershed management, Pobox 115, Shahrekord, Iran ([elham.omidzadehardali@ugent.be](mailto:elham.omidzadehardali@ugent.be))
23. EP: University of Bucharest, Research Centre in Systems Ecology and Sustainability, Splaiul Independentei 91-95, 050095 Bucharest, Romania ([elena.preda@g.unibuc.ro](mailto:elena.preda@g.unibuc.ro))
24. IR: Shahrekord University, Department of Rangeland and Watershed management, Pobox 115, Shahrekord, Iran ([irajrahimi93@gmail.com](mailto:irajrahimi93@gmail.com))

25. DR: Zoological research museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany ([d.rohwedder@leibniz-zfmk.de](mailto:d.rohwedder@leibniz-zfmk.de))
26. RR: Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster LA1 4AP, UK ([rjr@ceh.ac.uk](mailto:rjr@ceh.ac.uk))
27. EMS: University of Oxford, Department of Zoology, South Parks Road, Oxford, OX1 3PS, UK ; University of Lancaster, Lancaster Environment Centre, Lancaster LA1 4YQ, UK ([eleonor.slade@zoo.ox.ac.uk](mailto:eleonor.slade@zoo.ox.ac.uk))
28. LS: MTA Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4., H-2163 Vácrátót, Hungary; MTA Centre for Ecological Research, GINOP Sustainable Ecosystem Research Group, Klebelsberg u. 3., H-8237 Tihany, Hungary; Szent István University, Doctoral School of Environmental Sciences, Páter Károly u. 1., H-2100 Gödöllő, Hungary ([somay.laszlo@okologia.mta.hu](mailto:somay.laszlo@okologia.mta.hu))
29. PT: Shahrekord University, Department of Rangeland and Watershed management, Pobox 115, Shahrekord, Iran ([pejman.tahmasebi@nres.sku.ac.ir](mailto:pejman.tahmasebi@nres.sku.ac.ir))
30. SZ: GEOLAB, Via Case di Dozza, 22 40026 Imola (BO) , Italy ([stefanoziani@alice.it](mailto:stefanoziani@alice.it))
31. MHO: Ghent University, Department of Biology, TEREC, K.L. Ledeganckstraat 35, 9000 Gent, Belgium; Research Institute for Nature and Forest, Havenlaan 88/73, 1000 Brussels, Belgium ([maurice.hoffmann@inbo.be](mailto:maurice.hoffmann@inbo.be))

**Running title**

Dung removal and secondary seed dispersal by dung beetles

**Corresponding author**

Tanja Milotić ([tanja.milotic@inbo.be](mailto:tanja.milotic@inbo.be))

## Abstract

**Aim** In several ecosystems, the diversity of functional species traits has been shown to have a stronger effect on ecosystem functioning than taxonomic diversity alone. However, few studies have explored this idea at a large geographic scale. In a multi-site experiment, we unravelled the relationship between ecosystem function and functional completeness of species assemblages using dung beetles as a model group, focusing on dung removal and secondary seed dispersal.

**Location** 17 grassland locations across the Western Palaearctic.

**Methods** We used a randomized block design with different enclosure types to control the dung and seed removing activities of individual functional groups of the local dung beetle assemblage. We classified dung beetle species according to resource specialisation and into functional groups based on dung processing behaviour (dwellers, tunnellers, rollers) and body size (small, large). Additionally, we assessed the role of other soil macro-invertebrates. By sampling the dung beetle community and measuring the remaining dung and seeds after the experiment, the impact of each functional group was estimated.

**Results** Dung beetle assemblages differed along a north-south and east-west gradient. Dwellers dominated northernmost sites, whereas at lower latitudes we observed more tunnellers and rollers indicating a functional shift. Resource specialists were more abundant in southern and eastern areas. Overall, functional group diversity enhanced dung removal. More dung (+46.9%) and seeds (+32.1%) were removed in the southern sites and tunnellers and rollers were more effective. At the northernmost sites, where tunnellers were scarce or absent, other soil macro-invertebrates removed the majority of dung.

**Main conclusions** The conservation of functionally complete dung beetle assemblages is crucial to maintain the ecosystem functions provided by dung beetles. Given the latitudinal variation in functional group diversity, it is reasonable to expect compositional changes due to climate change. These changes could lead to increased dung removal and a higher secondary seed dispersal rate in northern regions.

**Key words** ecosystem service, ecosystem function, latitudinal gradient, longitudinal gradient, multi-site experiments, Scarabaeidae

## Introduction

The on-going loss of biodiversity highlights the importance of gaining insight into the relationship between species richness and ecosystem functioning (Larsen *et al.*, 2005; Duffy *et al.*, 2017). Even more disruptive than the loss of a single species is a functional shift in species assemblages. When species with unique traits disappear we would expect significant changes in ecosystem functioning and restructuring of ecological pathways (Barnes *et al.*, 2014). Many studies highlight the importance of facilitation or niche complementarity and the value of multi-species assemblages for specific ecosystem functions (Cardinale *et al.*, 2002). However, many of these studies have been criticized for their artificial and restricted species combinations and the strictly controlled abiotic environment (Naeem & Wright, 2003). In addition to these controlled (*ex situ*) lab experiments, large-scale field studies are necessary to explore the underlying mechanisms in a natural context. Field experiments are indispensable to verify the predictive ability of down-scaled lab experiments, for example as recently applied by Duffy *et al.* (2017) to link biodiversity and productivity using real world data.

In this study, we used dung beetles (Coleoptera: Scarabaeidae) as a focal taxon. Due to their broad geographic distribution and presence in all kinds of terrestrial habitats, dung beetles form a group well-fitted to field studies. Dung beetles use dung for feeding and breeding and it is relatively easy to measure dung removal by dung beetles in a standardized way. In ecosystem functioning research, dung removal can be applied as a direct measure for the relationship between ecosystem functioning and the functional completeness of dung beetle communities (Spector, 2006). Dung beetles can be classified into three major functional groups containing species with the same functional traits with regard to the direction of dung transport during nesting: tunnellers (paracoprids) make vertical shafts beneath dung pats, rollers (telecoprids) transport dung in a combined horizontal and vertical movement by rolling a dung ball a certain distance until burying it shallowly, and dwellers (endocoprids) reside within the original dung deposit (Doubé, 1990). Another distinction can be made based on resource specialisation level, with generalists using different dung types and specialists only attracted to a specific dung type. Both the relative abundance of different functional groups and the intensity of resource specialisation are linked to geography and climate. Dwellers and resource generalists are dominant in northern communities and increasing numbers of tunnellers, rollers and resource specialists are found at lower latitudes (Hortal *et al.*, 2011). The distribution of dung beetle species is closely linked with minimum temperature (Lobo *et al.*, 2002; Menéndez & Gutiérrez, 2004). An increase in mean minimum temperature due to global warming might affect the species structure and functional composition of local dung beetle assemblages and cause an elevational migration of dung beetles in mountain ranges (Menéndez *et al.*, 2014). Functional group richness and species composition of dung beetle assemblages strongly affect key ecological functions such as dung removal and decomposition (O'Hea *et al.*, 2010), secondary dispersal of seeds already present in dung (Slade *et al.*, 2007) and subsequent seed germination (D'hondt *et al.*, 2008). Hence, spatial variation in these ecosystem functions as provided by dung beetles seems plausible.

Due to the use of dung during feeding and nesting, dung beetles have an impact on several ecologically and economically valuable ecosystem functions and services (Beynon *et al.*, 2015) such as nutrient cycling (Sitters *et al.*, 2014) and bioturbation (Brown *et al.*, 2010). Furthermore, dung beetles are of great relevance for plant dispersal ecology as they facilitate secondary seed dispersal (Andresen, 2002). Larvae and adult individuals of dung beetles do not feed on the seeds present in dung but bury those seeds unintentionally (Nichols *et al.*, 2008). Therefore, the magnitude of seedling competition is

lowered since seeds are transported away from an environment which may contain high densities of endozoochorously dispersed seeds (Andresen & Levey, 2004).

Despite the global distribution of dung beetles, the majority of studies on the role of dung beetles in ecosystem functioning focus either on tropical and subtropical regions or are conducted in agricultural landscapes or microcosms (Nichols *et al.*, 2007; Slade *et al.*, 2017). In particular, studies in semi-natural landscapes in the Western Palaearctic region are scarce. To fill this gap, we conducted a large-scale field experiment at multiple sites in various biogeographic regions across the Western Palaearctic. Here we asked the following questions: (1) How are dung beetle functional assemblages affected by “geography” (i.e., latitudinal and longitudinal trends) and climate variables?; (2) How does the relative abundance of resource specialists and generalists relate to geography?; and (3) How does functional group diversity among dung beetles affect dung removal and secondary seed dispersal?

We estimated the contribution of each functional group to the ecosystem functions of dung removal and secondary seed dispersal. We locally manipulated the number of functional groups by using different enclosure types that inhibited the dung and seed removing activities of specific combinations of functional groups of the local dung beetle assemblage. Simultaneously, we sampled the local dung beetle assemblage using different dung types as bait.

## Methods

### *Study sites*

We carried out a multi-site experiment on 17 study sites across 10 countries in the Western Palaearctic realm (figure 1A and table S1). Each study site was assigned to a biogeographic region according to Udvardy (1975). The experiment was replicated both on a spatial scale by selecting study sites within the same biogeographic region (table S2) and a temporal scale by repeating the experiment in 2013, 2014, 2015 and/or 2016. All experiments and sampling were carried out during the main activity period of dung beetles in each region (table S3). The predominant vegetation type at the study site was (semi-)natural grassland. All study areas had been grazed by domestic and/or wild ungulates for at least two years prior to the experiment.

### *Dung beetle classification*

Dung beetles were strictly defined as those species of the superfamily Scarabaeoidea that feed on dung in both the larval and adult phases (Hanski & Cambefort, 1991). Ecosystem functions such as dung decomposition and secondary seed dispersal are most likely affected by the amount of dung taken and the direction of dung transport. In our study, dung beetle species were assigned to one of the three main dung beetle functional groups: dwellers, tunnellers or rollers (Milotić *et al.*, 2018). As the amount of dung transport is strongly correlated with beetle size (Horgan, 2001), beetles were further subdivided into size classes, as either small or large (body size smaller or larger than 1 cm). All Western Palaearctic dwellers are considered small species (personal communication D. Mann) and

were therefore not classified according to size. Other soil macro-invertebrates, such as earthworms, ants, termites and isopods, are also often major dung feeders or decomposers (e.g., Gittings *et al.* (1994)) with a similar dung removal strategy to tunnellers. Therefore, we defined a sixth and seventh functional group composed of either small or large soil macro-invertebrates. In addition, we made a second classification of dung beetle species according to resource specialization with a distinction between resource generalists and specialists based on the number of dung types used for feeding (specialists: 1-2, and generalists: > 2 dung types; table S5).

### *Experimental design*

We designed eleven enclosure types containing a standardized dung portion. By combining ground screens, vertical walls, and/or ceilings the dung removing activity by different combinations of functional groups was prevented (figure 1B). The components of the enclosures were made of plastic square mesh, and the mesh size determined the size class of the invertebrates that were able to remove dung from the experimental unit. We used 1 cm<sup>2</sup> mesh to exclude large individuals (while still including small individuals), and 1 mm<sup>2</sup> mesh to exclude all macroinvertebrate activity. In treatments lacking ground screens, ceilings or walls, tunnellers and rollers of all size classes were able to translocate dung. As dung beetles most often reach their feeding source by flying (Larsen & Forsyth, 2005), all treatments without ceilings allowed the entrance of any dung beetle functional group, but the removal of dung by tunnellers and rollers was prevented by the use of ground screens and walls. In study areas where no rollers occur we used a reduced set of enclosure types. The same basic set of 5 enclosure types was built at each site, while in areas where rolling species could occur 6 more enclosure types were constructed. We replicated each experimental treatment six times for each dung type and we grouped units using the same dung type in blocks. Within each block, we set up experimental units in a fully randomized design. Individual experimental units were 60 cm apart, while different blocks were at least 2 m apart (figure 1C).

### *Dung removal and secondary seed dispersal experiments*

As the presence of anthelmintic residues in dung affects the attractiveness of dung to dung beetles (Errouissi & Lumaret, 2010), we collected dung from animals that had not been treated in the preceding six weeks. This duration is considered long enough to suppress these attractive effects (Beynon, 2012).

Standardized amounts of dung (table S3) were put in the centre of each experimental plot and left on site for one month, after which the remaining dung was collected and quantified.

At the start of the experiment, fresh subsamples of each dung batch were taken and weighed for use as a reference sample. Subsequently, reference samples were oven-dried (80 °C) and the dry weight was measured ( $M_{initial}$ ). At the end of the experiment, the remaining dung in the experimental units was collected, oven-dried and the dry mass was measured ( $M_{final}$ ).

Dung removal ratio (DRR) was calculated as:



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

In a subset of study sites, secondary seed dispersal by dung beetles was simultaneously measured during the dung removal experiments. Therefore, ten seeds of each of three seed classes (small, medium, and large) were mixed with the dung portions at the start of the experiment ( $S_{initial}$ , table S4). In order to facilitate the retrieval of seeds at the end of the experiment and to prevent germination during the experiment, seeds were pre-treated using fluorescent paint and heating using the methodology of Milotić *et al.* (2017). At the end of the experiment, the dried dung was crumbled and the remaining seeds were counted ( $S_{final}$ ).

Seed dispersal ratio (SDR) was calculated for each seed size class as:

$$SDR = \frac{S_{initial} - S_{final}}{S_{initial}} \quad (2)$$

### *Dung beetle sampling*

During each experimental run, the dung beetle community was sampled in pitfall traps baited with the dung types used in the experiments. In 2013 and 2014, two types of pitfall traps were used in order to achieve a complete representation of dung beetle diversity and abundance. The first trap type consisted of 5 small containers surrounding a central dung pile, while the second trap type was one large container with dung on top (figure 1D). During the experiments in 2015 and 2016, sampling effort was lowered by using only the latter trap type (Milotić *et al.* (2018)). Traps were set up randomly between the experimental units with six replicates per dung type (figure 1C). In order to minimize interference with the early colonization phase in the experimental plots, traps were put in operation one week after the start of the experiments. We emptied traps weekly for three weeks. For each dung beetle species sampled, we counted the total number of individuals per trap and sampling date.

## **Data analysis**

### *Dung beetle diversity*

To measure the effects of geography and climate variables on species richness and dung beetle abundance, we used generalized linear modelling (GLM). Climate variables during the sampling periods were downloaded from the monthly summary observations map of (NOAA, 2016) by selecting the nearest climate station for each study site. Species richness was calculated as the sum of species sampled in each trap, while dung beetle density was the total number of dung beetles in each trap. Full GLMs were built using either species richness or dung beetle density as the response variable and latitude, longitude, mean temperature and total monthly precipitation as predictor variables. We used a combined forward and backward stepwise model selection approach for simplifying the model based on AIC-values on all GLM models. As we were particularly interested in the distribution of dung beetle functional groups, we made additional models for each dung beetle functional group using density as a response variable.

In order to create an overview of the local species richness, we calculated Shannon Weaver diversity indices and evenness for each study site (Hill, 1973). We transformed the Shannon Weaver index to the effective number of species according to the method of Jost (2009).

The relation between resource specialization and geography (research question 2) was explored using linear regression models with the percentage of resource specialists (based on the total dung beetle density) as the response variable and latitude, longitude, mean temperature and total monthly precipitation as predictor variables.

### *Dung removal and secondary seed dispersal*

In order to get an overview of the regional differences in dung removal by the complete local fauna assemblage, we selected the experimental plots without any walls or ground screens. Using this subset of the experiment data, we built a GLM with DRR as the response variable and geography (latitude, longitude) and climate (mean temperature, total monthly precipitation) as predictor variables. In the next step, the effects of incomplete dung fauna assemblages on ecosystem functioning was explored by GLM using the complete experimental dataset. Four different models were built with either DRR (equation 1) or SDR for small, medium or large sized seeds (equation 2) as the response variable and with geography (latitude, longitude), climate (mean temperature, total monthly precipitation), dung fauna metrics (total dung beetle abundance, the proportions of each dung beetle functional group (dwellers, small tunnellers, large tunnellers, and small rollers), and the presence or absence of soil macro-invertebrates (small or large) as predictor variables.

In order to gain further insight in the relative contribution of each functional group to the ecosystem function of dung removal, we built hierarchical partitioning models for each study site. Using this multiple regression technique, we were able to estimate the independent effect of each functional group on dung removal. We obtained significance levels for the independent effect of each predictor variable after running 1000 randomization tests.

To test the validity of our methodology for studying seed dispersal and to test whether dung beetles actively select dung particles with or without seeds, we performed simple linear analyses with SDR as the response variable and DRR as the predictor variable. All analyses were performed in R version 3.4.2. (R Core Team, 2017). The 'hier.part' package was used to build hierarchical partitioning models (Walsh & Mac Nally, 2013).

## **Results**

### *Dung beetle assemblage*

In total, we sampled 34,994 specimens belonging to 94 Scarabaeoidea species. We assigned species to four of the five predetermined functional groups: dwellers, large and small tunnellers and small rollers (52, 8, 32 and 2 species, respectively). Apart from the study sites in the Mediterranean sclerophyll region (La Fage) and the Caucaso-Iranian highlands (Shahrekord), no rollers were recorded and even in these sites their share in the overall dung beetle community was very small. In addition, the distribution of large tunneller species of the Geotrupidae family was mainly limited to the sites in the Atlantic, Central European highlands, and Pannonian region (table S5). We found the highest species diversity at Bugac in the Pannonian region, while individual sampling units contained most specimens at the La Fage site in the Mediterranean region (table S6). Overall, more species were found in the western study sites and dung beetles were more abundant in western and southern areas (figure 2). Study sites with a high mean temperature during the experiments contained more species, whereas a negative relationship was found between the total monthly precipitation and species richness or dung beetle abundance. Similar trends were found for the abundance of each of the functional groups separately, with the exception of the negative relationship between temperature and the abundance of large tunnellers. Furthermore, the few species found in northern areas are mostly dung resource generalists, whereas richer dung beetle assemblages at lower latitudes are more variable and contain a greater proportion of resource specialists. In general, the proportion of resource specialists is negatively affected by precipitation (figure 2 and table S7).

#### *Dung removal and secondary seed dispersal*

Dung removal ratios clearly differed between regions when the local dung fauna was left intact (figure 3). More dung was removed at higher latitudes, while the opposite effect was found for increasing longitudes. At higher mean temperatures, dung removal ratios were lower, whereas a positive relation was found between dung removal and total monthly precipitation.

The presence of dwellers, small tunnellers, small rollers and small and large macro-invertebrates had a clear positive effect on dung removal, whereas the presence of large tunnellers did not result in increased dung removal (table 1). At the study site level, both large and small tunnellers were significant dung removers when abundant (e.g., in the Hungarian sites and southern European sites) (figure 4). In the Mediterranean region, rollers were significant dung removers whereas dwellers had an important role in dung removal at The Zwin, Steinbühl, Tähtvere parish, Moor House National Nature Reserve, Shahrekord, Bayreuth, Bavarian Forest National Park, and Bugac. Soil macro-invertebrates were particularly important in Le Chesnoy, The Zwin, Swindon, Tange Sayad, Bayreuth, and Lygra.

Likewise, the presence of functional groups affected secondary seed dispersal. More seeds were dispersed when tunnellers were able to enter the experimental plots, whereas macro-invertebrates other than dung beetles had the opposite effect. Furthermore, dwellers generally had a negative effect on seed dispersal. Mean monthly temperature and total precipitation had a strong positive and negative effect, respectively, for most seed size classes (table 1). We found strong positive correlations between secondary seed dispersal and dung removal in all studied biogeographic regions (figure S1), although there were differences among seed sizes with a higher dispersal ratio for smaller seeds.

## Discussion

### *Functional composition*

Northernmost regions were dominated by dwellers, while tunnellers and rollers become more prominent with decreased latitude. This corresponds well with the known biogeographic distribution of dung beetle functional groups in the northern temperate hemisphere (Hanski & Cambefort, 1991), although roller species were scarce in our study. In general, however, Geotrupidae are known to be present in northern areas such as the British Isles and Scandinavia (Rosenlew & Roslin, 2008). Although species diversity at most sites fell within the range of expectations (Hortal *et al.*, 2011), it is still possible that our sampled dung beetle assemblages were incomplete at the time of sampling due to stochastic variations in weather conditions, phenological population peaks, or the abundance of resources in the vicinity. Another explanation for rather low species diversity and the limited number of functional groups in some regions might be the global decline in dung beetle abundance and diversity. Roller species in particular have declined in southern Europe since the 1950s, in relation to land use changes, the use of anthelmintics and increasing urban development (Carpaneto *et al.*, 2007). The trend of increasing complexity in dung beetle assemblage composition with decreasing latitude, and to a minor extent with increasing longitude, could be the result of the location of the 0°C isotherm both currently and during the last-glacial period (Hortal *et al.*, 2011). Hence, the current distribution of dung beetle species in the Western Palaearctic is most likely defined by the location of refuge areas during the last glacial period, resulting in high levels of endemism and specialism in southern Europe (Lumaret & Lobo, 1996). Due to the close link between functional groups' spatial distribution and temperature, a global increase in temperature might result in more diverse dung beetle assemblages in northern regions, while a lowered diversity is expected in southern regions of the Western Palaearctic (Dortel *et al.*, 2013).

### *Ecosystem functions of dung removal and secondary seed dispersal*

The presence of dung beetles results in improved ecosystem functioning in terms of dung removal and secondary seed dispersal. Dwellers, being the most abundant functional group in the northern regions, did not contribute very much to dung removal in these regions. Dwellers in the Iberian highlands on the other hand, removed a significant amount of dung although the functional group was underrepresented in the sampled dung beetle assemblage. Possibly, larval development and dung consumption by dweller larvae are faster at these sites compared with the northern sites, and could be related to higher summer temperatures (Stevenson & Dindal, 1985). Furthermore, the presence of tunnellers in southern regions might change the physical properties of dung into a more suitable habitat for dwellers, for example by increasing the dung surface. However, our method to measure dung removal by dwellers did not exclude other airborne coprophilous fauna that colonised the dung. With the exception of the covered treatment plots, none of the other treatments prevented oviposition by dung flies. As the larvae of dung-breeding flies play an important role in the dung ecosystem and are highly abundant and globally distributed (Hanski & Cambefort, 1991), the measured dung removal might be partially attributed to dung flies. Furthermore, we should note that tunnellers

and rollers were also able to *feed* on the dung in the roofless treatment plots designed to measure the impact of dweller species, but were not able to *move* dung by tunnelling or rolling.

Many other soil macro-invertebrate groups are often found in dung, but are rarely considered as true members of the dung community (Floate, 2011). Such species are most often found in the later stages of dung degradation and are often casual visitors from adjacent habitats (e.g., woodlice (Isopoda), springtails (Collembola), and earthworms (Oligochaeta)). Especially in the cool and wet climate of northern Europe, earthworms can fulfil an important role in dung decomposition (Gittings *et al.*, 1994) although their overall contribution is much lower compared with large tunnelling species (Kaartinen *et al.*, 2013). According to Rosenlew and Roslin (2008), more dung is removed by large tunnellers compared with earthworms when both groups were present. However, despite the fact that earthworms and tunnellers perform similar roles in ecosystem functioning by vertically transporting dung (increasing soil respiration, and water and carbon content (Hendriksen, 1997)), these groups are not equivalent as earthworms tend to remove less dung but bury deeper (Holter, 1979). In the Mediterranean region, small rollers removed a disproportionately high amount of dung, which contrasts with some research results from (sub)tropical regions where tunnellers are considered the most important dung removers (e.g., Davis (1996), Slade *et al.* (2007)) and where larger beetles account for more dung removal (Braga *et al.*, 2013). The high contribution of rolling species in southern Europe also highlights the potential negative consequences of the on-going decline in the abundance and diversity of roller species in this region for the ecosystem functions measured here (Carpaneto *et al.*, 2007).

The strong positive relationship between secondary seed dispersal and dung removal suggests that dung beetles did not distinguish between seed-containing dung and seed-free dung. This result has been found previously for relatively small seeds (e.g., 4 mm seeds in Andresen (2002), 3.5 mm in Slade *et al.* (2007)), although the number of buried seeds increased with dung pat size and dung beetle size (Andresen & Feer, 2005). Moreover, the relationship might switch from positive to negative, if the proportion of seeds present in the dung is higher (Shepherd & Chapman, 1998). In contrast to most earlier studies of secondary seed dispersal by dung beetles, we used real seeds instead of plastic proxies. Although this approach is ecologically more realistic, dung beetles might handle real seeds differentially not only with respect to size but also with respect to morphology (shape, seed appendages) and smell. As a consequence of the applied experimental setting, a portion of missing seeds could have been removed (*dispersed*) and/or destroyed (*predated*) by individuals of other animal groups than the studied focal groups (e.g., ants, rodents, birds) (Andresen & Levey, 2004; Hulme & Kollmann, 2004).

Secondary seed dispersal by dung beetles may have a direct impact on the reproductive success of plants (Shepherd & Chapman, 1998; Nichols *et al.*, 2008). The distribution of seeds away from their original dropping site can help lower the level of competition between seedlings (Andresen & Levey, 2004) and the impact of above-ground seed predators (Manzano *et al.*, 2010). However, one of the main determinants of whether seeds germinate after secondary dispersal is the depth at which they are buried (Andresen & Feer, 2005), which differs between dung beetle species (D'hondt *et al.*, 2008) and the specific germination requirements of the plant species (Limón & Peco, 2016). Rollers might provide optimal conditions for successful germination as they move seed-containing dung away in a horizontal direction and bury dung shallowly. Similarly, earthworms deposit consumed dung as casts in the soil in the upper 2 cm, where most plant species should be able to germinate (Hendriksen, 1997).

By contrast, many tunnellers make deep vertical shafts below the dung pat (up to 150 cm depth; e.g., *Typhaeus typhoeus* (L.); Brussaard (1985)) probably suppressing germination (Fenner & Thompson, 2005). Dwellers might release seeds from the dung substrate, thus improving light availability but in many cases they will not provide as much seed-soil contact as predominantly burying species, leading to lower water availability for germination (Fenner & Thompson, 2005).

The conservation of functionally complete species assemblages is essential in order to maintain ecosystem functioning (Manning *et al.*, 2016). Given the clear north-south shift in functional group composition and the generally high dispersal ability of dung beetles, we can assume significant changes in functional group composition due to climate change. This could lead to an increased dung removal and secondary seed dispersal rate in the northern regions, while in southern regions the combination of more frequent and longer heat waves and a drier climate might result in the disappearance of vulnerable functional groups (e.g., rollers which typically make nests close to the surface) and associated ecosystem functions (Menéndez *et al.*, 2014; Slade & Roslin, 2016). Experimental manipulations of local dung beetle assemblages (e.g., through the introduction of new species in a mesocosm experiment) could provide further knowledge of how change in dung beetle assemblages affect ecosystem functioning.

## Acknowledgments

This study is the result of a pan-European multi-site project, financially supported by the **ALTER-Net** consortium, Europe's Ecosystem Research Network. The project was co-financed within their multi-site research programme. Yves Israel, Robbe De Beelde, Viki Vandomme, Angelica Alcantara, Linda Stevens, Tessa Van Santen and Martine Van Hove provided practical and logistical assistance in cutting gauze and sending the experimental material to the participants. We thank Stefan Van Damme for testing the experimental materials and fine-tuning the experimental protocol in a pilot study. JAN was funded by COLCIENCIAS (Colombia).

We thank Eva Cuesta, María Leo Montes, Ana M.C. Santos, Indradatta de Castro, Joaquin Hortal, Andrew Smithson, Matthew Rowlinson, Sally-Ann Spence, Berrycroft Farm, Capucine Tourret, Yoann Despres, H el ene Beno it-Valiergue, Claire Debulois, Rachel Barrier, Catherine Menuet, M elanie Picard, Yves Boscardin, Marie Hauso, Joanne Inchbald, Sayuri Kiyota Beltran, Wilhelm Karch, Anne Drozynski, Anna Paquet, Anne Raber, Florian Samsony, Philipp Wagner, Helmut Hackl, Josef Nu hard, Dennis M uller, Ferenc Sipos, Zolt an Vajda, M ark Lucza, Irja Kivim agi, Marius Bujor, Mirona Zovot, Tudor Racoviceanu and Mr. Darakhshon for their assistance during the field work.

We thank the Community of Madrid, the Natural Protect Area of Soto de Vi uelas, the Regional Park of Cuenca Alta del Manzanares, Environmental Change Network, LEGTA "Le Chesnoy - Les Barres", Sara Parisot, the Agency for Nature and Forest (ANB), the Heathland Centre (Lynghesenteret), NABU Kirchheimbolanden, LBV Lindenhof, Bayreuth, and the Braila Research Station for providing access and logistical help at the study sites. Local permits were obtained for entering the study areas and for sampling insects.

We thank two anonymous reviewers and the handling editor for their useful suggestion on an earlier version of this manuscript.

## Data Accessibility statement

All data are available as open data. Dung beetle sampling data have been published as a sampling event dataset on GBIF (<https://www.gbif.org/dataset/bcbfd319-8813-4b6d-b529-07dc5a6ccf56>). Results of the dung removal and secondary seed dispersal experiments can be accessed at Zenodo (<https://zenodo.org/record/1115523#.WjEpHIXiapo>).

## Bio sketch

Tanja Milotić designed and completed this study during her PhD at the Terrestrial Ecology Unit (TEREC) of Ghent University, Belgium. Her research focuses on the dispersal of plant seeds through endozoochory and the effects of dung beetles on this process.

## Author contributions

TM and MHo designed the study and applied for financing in the multi-site research program of the ALTER-Net consortium. TM, CB, CE, AE, MH, JM, JAN, RM, JS, RA, TB, IB, JB, JC, GB, PJR, MK, EM, AM, EA, EP, IR, RR, EMS and LS installed the experiment and collected field data. TM, MH, JM, JAN, RM, JB, CC, PJR, MK, EM, GM, AM, DR, EMS, LS and SZ identified dung beetles. TM did all analyses and led the writing in close cooperation with CB, CE, AE, MH, JM, JAN, RM, JS, JC and MHo. All authors discussed the analysis results and their interpretations in the manuscript.

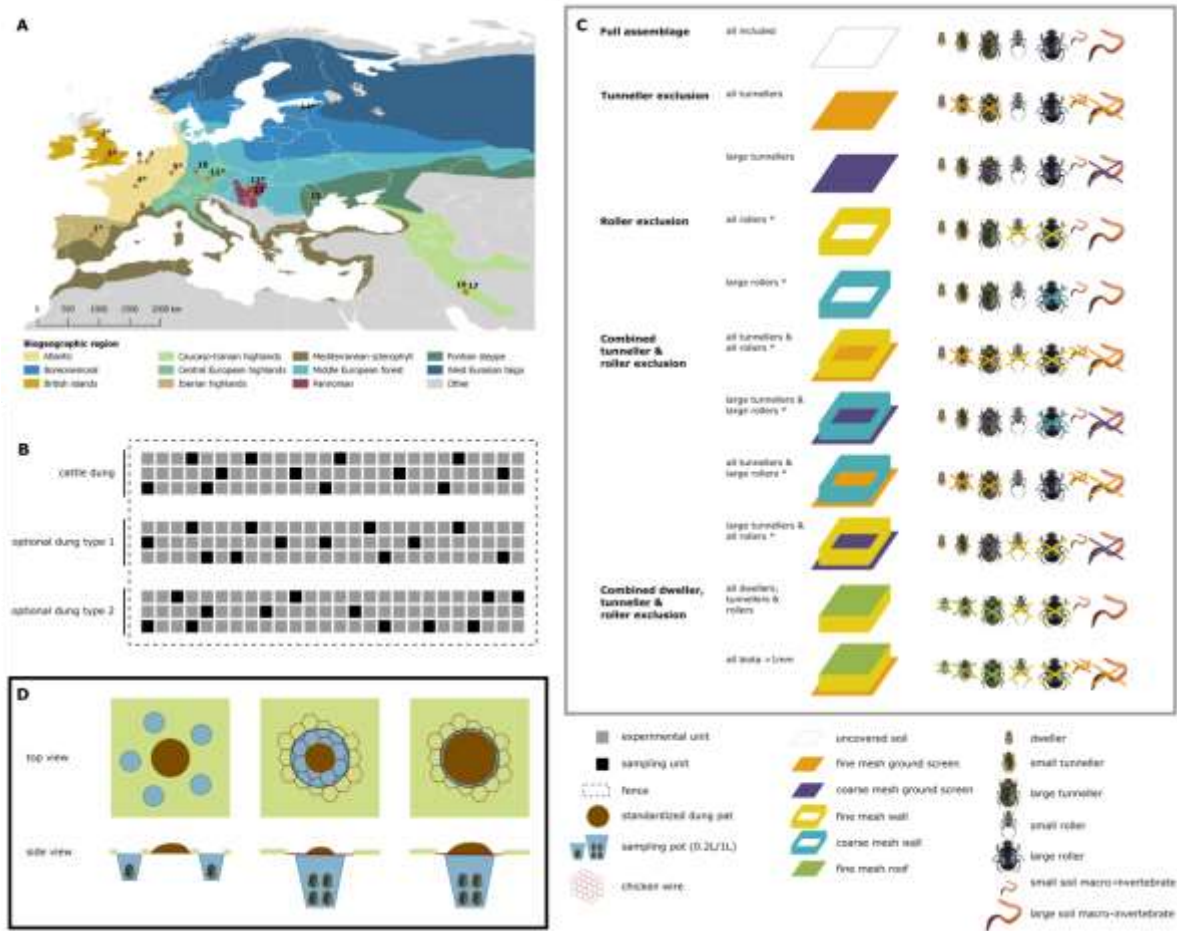
## Tables

**Table 1** – Model results of the generalized linear models for dung removal and seed dispersal by dung beetles in the Western Palaearctic. Dung removal and the dispersal of small, medium or large-sized seeds were used as response variables and geography (latitude and longitude), climate (mean temperature and total monthly precipitation, total dung beetle abundance, the proportion of each dung beetle functional group (dwellers, small tunnellers, large tunnellers, and small rollers), and the presence or absence of soil macro-invertebrates (small and large) as predictor variables. Only those variables that were retained after a combined forward and backward model selection procedure based on AIC are shown.

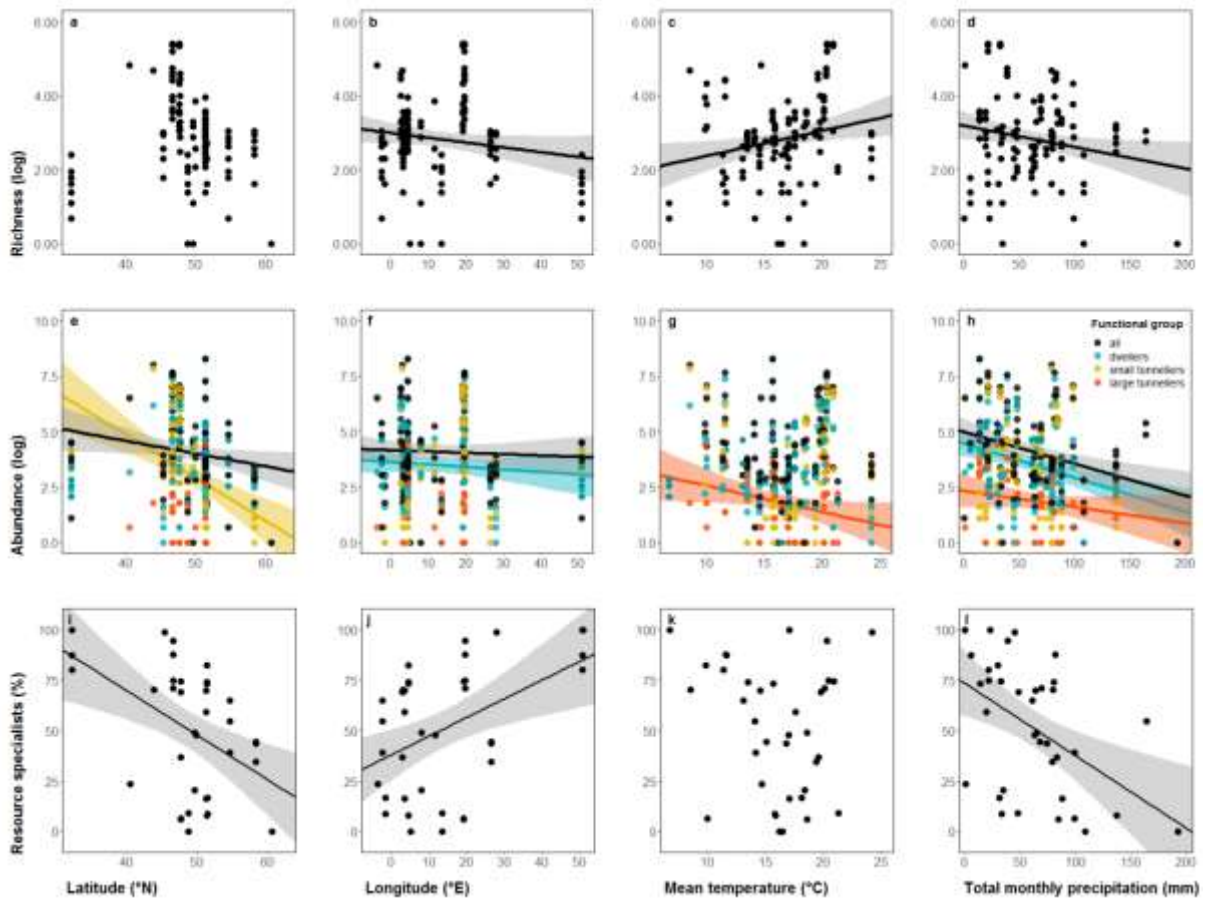
<b>Response variable</b>	<b>Predictor variable</b>	<b>t-value</b>	<b>p-value</b>
dung removal ratio	intercept	12.723	<0.001
	latitude	-6.158	<0.001
	longitude	-10.702	<0.001
	mean temperature	-6.823	<0.001
	total monthly precipitation	3.525	<0.001
	dung beetle abundance	7.225	0.073
	dwellers	2.440	<0.001
	small tunnellers	4.049	0.015
	small rollers	4.754	<0.001
	small soil macro-invertebrates	8.914	<0.001
	large soil macro-invertebrates	1.793	<0.001
small seed removal	intercept	3.880	<0.001
	longitude	-9.661	<0.001
	mean temperature	19.141	<0.001
	total monthly precipitation	-11.086	<0.001
	dung beetle abundance	4.366	<0.001
	dwellers	-3.537	<0.001
	small tunnellers	4.095	<0.001
	large tunnellers	5.649	<0.001
	small soil macro-invertebrates	-3.830	<0.001
medium seed removal	intercept	3.895	<0.001
	latitude	-7.431	<0.001
	longitude	-8.312	<0.001
	mean temperature	21.373	<0.001
	dung beetle abundance	7.546	<0.001
	dwellers	-3.462	<0.001
	small tunnellers	2.723	<0.001
	large tunnellers	7.351	0.007
	small soil macro-invertebrates	-8.724	<0.001
large seed removal	intercept	-4.443	<0.001
	latitude	9.997	<0.001
	longitude	-6.235	<0.001
	mean temperature	2.102	0.036
	total monthly precipitation	-8.648	<0.001
	dwellers	2.737	0.006
	small tunnellers	-1.513	0.130
	small rollers	4.694	<0.001
	small soil macro-invertebrates	1.896	0.058



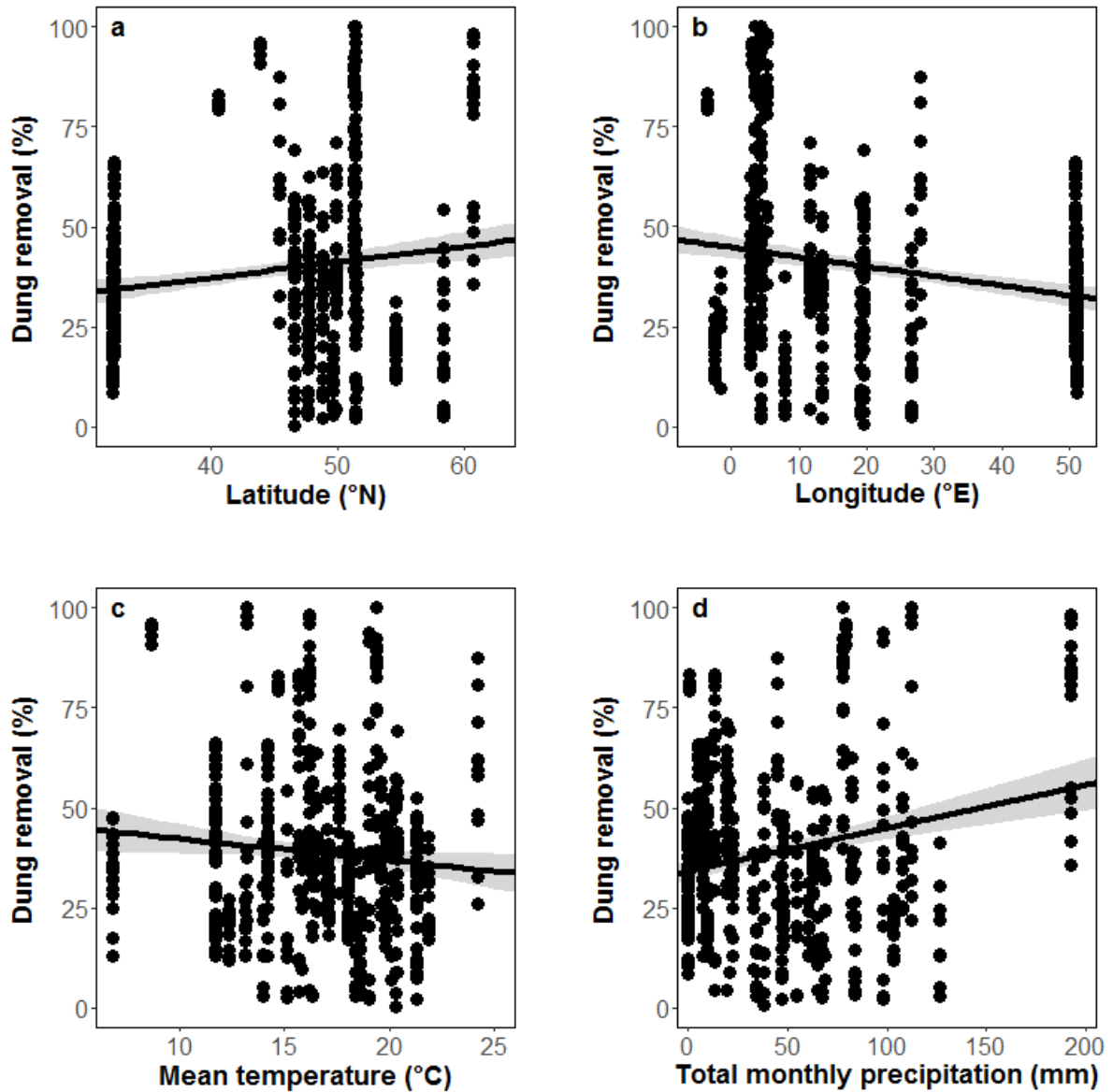
# Figures



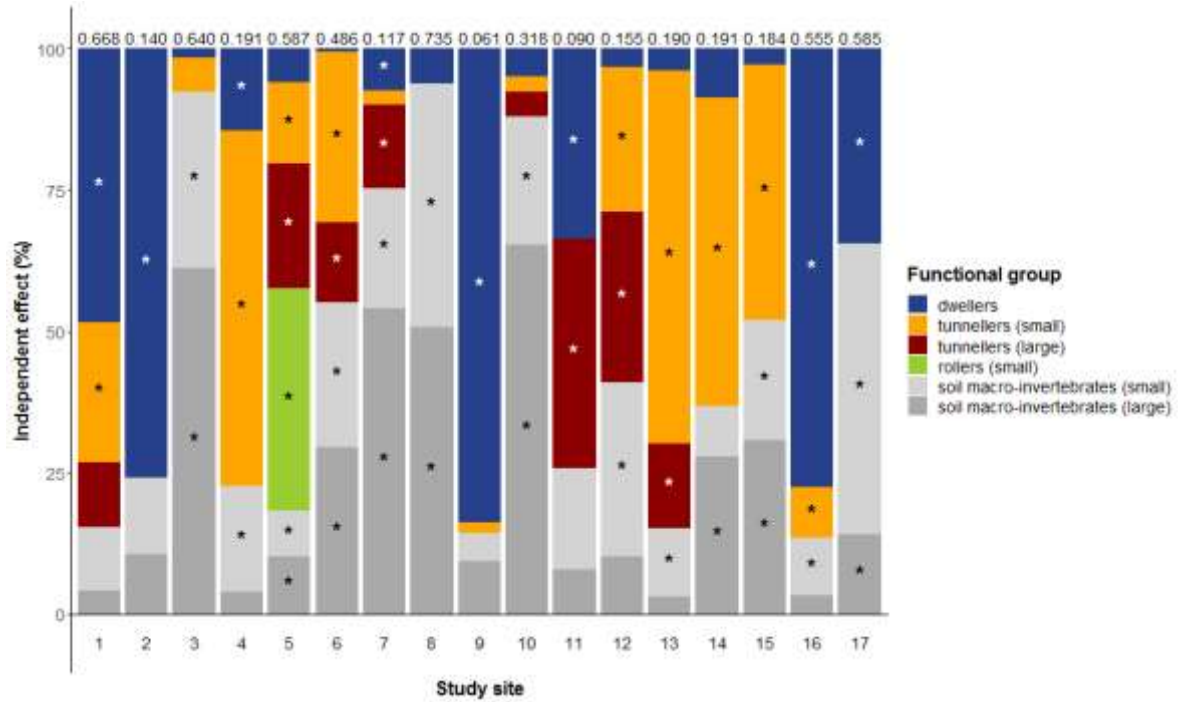
**Figure 1** – Set-up of the multi-site experiment estimating dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. **A**. Position of the study sites shown within biogeographic provinces as defined by Urdvary (1975); the digital base map was adapted from FAO Geonetwork (2015). See table S1 for site names and coordinates. At study sites marked with an asterisk, a reduced set of experimental treatments was installed as no rollers were expected to be present at these sites. **B**. Experimental design with a randomized distribution of 11 types of experimental units and 2 types of dung beetle sampling units. In the second year of the experiment sampling efforts were reduced with 1 sampling unit type in a similar set-up. Experimental and sampling units were grouped by dung types in a fenced experimental area. Cattle dung was used as a standard dung type. At most study sites, the experiment was replicated with up to two additional dung types. All experimental and sampling unit types were replicated six times per experimental run. **C**. Treatments used in the dung removal and seed dispersal experiments. In each treatment unit, a standard amount of dung was put in the center of the plot, and functional groups were excluded using ground screens, walls and/or roofs made of fine (1 mm<sup>2</sup>) or coarse mesh (1 cm<sup>2</sup>). For each treatment, functional groups unable to move dung are crossed out. The colors of the crosses refer to the colors of the building materials (see legend). Treatments excluding roller activity were not installed in regions with known roller absence and are indicated with an asterisk (\*). **D**. Sampling strategy with three different trap types consisting of: 5 small pitfalls surrounding a central dung pile (left), and 1 large pitfall covered with a dung ball in a nylon bag (middle) used in the first year of the experiment, and 1 large pitfall covered with a large unpacked dung pile (right) used in the second year.



**Figure 2** – GLM model results showing relationships between species richness, dung beetle abundance or the proportion of resource specialist (y-axes) and latitude (a, e, i), longitude (b, f, j), mean temperature (c, g, k), and total monthly precipitation (d, h, l). Model-predicted means (solid lines) and standard errors are plotted for significantly correlated variables. Full model results are provided in table S7.



**Figure 3** – Dung removal in complete dung fauna assemblages in the Western Palaearctic. Graphs show the relationship between the percentage of dung removed after one month and geographic (latitude (a), longitude (b)) and climatic variables (mean temperature (c), total monthly precipitation (d)). Significantly correlated variables after GLM analysis are plotted as solid lines with standard errors (grey). Full model results are provided in table S8.



**Figure 4** – Hierarchical partitioning results for dung removal by dwellers, tunnellers, rollers and soil macro-invertebrates in the Western Palaearctic. Displayed is the percentage of independent effect contributed by each functional group in each study site. Study sites are coded according to the codes in figure 1 and table S1 and are ordered by longitude. Asterisks indicate whether the contribution of a functional group is significant ( $p < 0.050$ ) in a particular study site. The level of significance of the independent contribution of each functional group was estimated using randomization tests based on 1000 permutations. On top of each bar  $R^2$  values of the total model is shown for each study site.

## References

- Andresen, E. (2002) Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology*, **27**, 257-270.
- Andresen, E. & Levey, D.J. (2004) Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, **139**, 45-54.
- Andresen, E. & Feer, F. (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. *Seed fate. Predation, dispersal and seedling establishment* (ed. by P.-M. Forget, J.E. Lambert, P.E. Hulme and S.B. Vander Wall), pp. 331-349. CABI, Oxon, UK.
- Barnes, A.D., Emberson, R.M., Krell, F.T. & Didham, R.K. (2014) The role of species traits in mediating functional recovery during matrix restoration. *PLoS ONE*, **9**, e115385.
- Beynon, S.A. (2012) Potential environmental consequences of administration of anthelmintics to sheep. *Veterinary Parasitology*, **189**, 113-124.
- Beynon, S.A., Wainwright, W.A. & Christie, M. (2015) The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry. *Ecological Entomology*, **40**, 124-135.
- Braga, R.F., Korasaki, V., Andresen, E. & Louzada, J. (2013) Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: A rapid assessment of ecological functions associated to biodiversity. *PLoS ONE*, **8**, e57786.
- 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.
- Brussaard, L. (1985) *A pedobiological study of the dung beetle Typhaeus typhoeus (Coleoptera, Geotrupidae)*, PhD Dissertation, Wageningen University, Netherlands.
- Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, **415**, 426-429.
- Carpaneto, G.M., Mazziotta, A. & Valerio, L. (2007) Inferring species decline from collection records: roller dung beetles in Italy (Coleoptera, Scarabaeidae). *Diversity and Distributions*, **13**, 903-919.
- 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.
- Davis, A.L.V. (1996) Seasonal dung beetle activity and dung dispersal in selected South African habitats: Implications for pasture improvement in Australia. *Agriculture, Ecosystems and Environment*, **58**, 157-169.
- Dortel, E., Thuiller, W., Lobo, J.M., Bohbot, H., Lumaret, J.P. & Jay-Robert, P. (2013) Potential effects of climate change on the distribution of Scarabaeidae dung beetles in Western Europe. *Journal of Insect Conservation*, **17**, 1059-1070.
- Doube, B.M. (1990) A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology*, **15**, 371-383.
- Duffy, J., Godwin, C. & Cardinale, B. (2017) Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, **549**, 261-264.
- Errouissi, F. & Lumaret, J.P. (2010) Field effects of faecal residues from ivermectin slow-release boluses on the attractiveness of cattle dung to dung beetles. *Med Vet Entomol*, **24**, 433-40.
- 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>. In:
- Fenner, M. & Thompson, K. (2005) *The ecology of seeds*. Cambridge University Press, Cambridge, UK.
- Floate, K.D. (2011) Arthropods in cattle dung on Canada's grasslands. *Arthropods of Canadian grasslands*, **2**, 71-88.
- Gittings, T., Giller, P.S. & Stakelum, G. (1994) Dung decomposition in contrasting temperate pastures in relation to dung beetle and earthworm activity. *Pedobiologia*, **38**, 455-474.

- Hanski, I. & Cambefort, Y. (1991) *Dung beetle ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Hendriksen, N.B. (1997) Earthworm effects on respiratory activity in a dung-soil system. *Soil Biology and Biochemistry*, **29**, 347-351.
- Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427-432.
- Holter, P. (1979) Effect of dung beetles (*Aphodius* spp.) and earthworms on the disappearance of cattle dung. *Oikos*, **32**, 393-402.
- Horgan, F.G. (2001) Burial of bovine dung by coprophagous beetles (Coleoptera: Scarabaeidae) from horse and cow grazing sites in El Salvador. *European Journal of Soil Biology*, **37**, 103-111.
- Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741-748.
- Hulme, P. & Kollmann, J. (2004) Seed predator guilds, spatial variation in post-dispersal seed predation and potential effects on plant demography: a temperate perspective. *Seed Fate* (ed. by P. Forget, J. Lambert, P. Hulme and S. Vander Wall), p. 432. CAB International, Wallingford, Oxfordshire.
- Jost, L. (2009) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427-2439.
- Kaartinen, R., Hardwick, B. & Roslin, T. (2013) Using citizen scientists to measure an ecosystem service nationwide. *Ecology*, **94**, 2645-2652.
- Larsen, T.H. & Forsyth, A. (2005) Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica*, **37**, 322-325.
- Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecological Letters*, **8**, 538-47.
- Limón, Á. & Peco, B. (2016) Germination and emergence of annual species and burial depth: Implications for restoration ecology. *Acta Oecologica*, **71**, 8-13.
- Lobo, J.M., Lumaret, J.P. & Jay-Robert, P. (2002) Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. *Global Ecology and Biogeography*, **11**, 265-277.
- Lumaret, J.P. & Lobo, J.M. (1996) Geographic distribution of endemic dung beetles (Coleoptera, Scarabaeoidea) in the Western Palaearctic region. *Biodiversity Letters*, **3**, 192-199.
- 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.
- Manzano, P., Azcárate, F.M., Peco, B. & Malo, J.E. (2010) Are ecologists blind to small things? The missed stories on non-tropical seed predation on feces. *Oikos*, **119**, 1537-1545.
- Menéndez, R. & Gutiérrez, D. (2004) Shifts in habitat associations of dung beetles in northern Spain: Climate change implications. *Ecoscience*, **11**, 329-337.
- Menéndez, R., González-Megías, A., Jay-Robert, P. & Marqués-Ferrando, R. (2014) Climate change and elevational range shifts: evidence from dung beetles in two European mountain ranges. *Global Ecology and Biogeography*, **23**, 646-657.
- Milotić, T., Quidé, S., Van Loo, T. & Hoffmann, M. (2017) Linking functional group richness and ecosystem functions of dung beetles - an experimental quantification. *Oecologia*, **183**, 177-190.
- Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A., Heurich, M., Müller, J., Noriega, J.A., Menendez, R., Stadler, J., Ádám, R., Bargmann, T.B., Bilger, I., Buse, J., Calatayud, J., Ciubuc, C., Boros, G., Jay-Robert, P., Kruus, M., Merivee, E., Miessen, G., Must, A., Ardali, E.O., Preda, E., Rahimi, I., Rohwedder, D., Rose, R., Slade, E.M., Somay, L., Tahmasebi, P., Ziani, S. & Hoffmann, M. (2018) Dung beetle assemblages, dung removal and secondary seed dispersal: data from a large-scale, multi-site experiment in the Western Palaearctic. *Frontiers in Biogeography*, **10**, e37829.

- Naeem, S. & Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, **6**, 567-579.
- Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M. & Vuline, K. (2007) Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation*, **137**, 1-19.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S., Favila, M.E. & TSRN (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, **141**, 1461-1474.
- NOAA (2016) *Climate maps*. Available at: <http://gis.ncdc.noaa.gov/maps/> (accessed August 2016).
- O'Hea, N.M., Kirwan, L. & Finn, J.A. (2010) Experimental mixtures of dung fauna affect dung decomposition through complex effects of species interactions. *Oikos*, **119**, 1081-1088.
- R Core Team (2017) *R: A language and environment for statistical computing. R version 3.4.2 (2017-09-28) -- "Short Summer"*. R Foundation for Statistical Computing.
- Rosenlew, H. & Roslin, T. (2008) Habitat fragmentation and the functional efficiency of temperate dung beetles. *Oikos*, **117**, 1659-1666.
- Shepherd, V.E. & Chapman, C.A. (1998) Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal of Tropical Ecology*, **14**, 199-215.
- 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.
- Slade, E.M. & Roslin, T. (2016) Dung beetle species interactions and multifunctionality are affected by an experimentally warmed climate. *Oikos*, **125**, 1607-1616.
- Slade, E.M., Mann, D.J., Villanueva, J.F. & Lewis, O.T. (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, **76**, 1094-1104.
- Slade, E.M., Kirwan, L., Bell, T., Philipson, C.D., Lewis, O.T. & Roslin, T. (2017) The importance of species identity and interactions for multifunctionality depends on how ecosystem functions are valued. *Ecology*, **98**, 2626-2639.
- Spector, S. (2006) Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): An invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin*, **5**, 71-83.
- Stevenson, B. & Dindal, D. (1985) Growth and development of *Aphodius* beetles (Scarabaeidae) in laboratory microcosms of cow dung. *The Coleopterists' Bulletin*, **39**, 215-220.
- Udvardy, M.D.F. (1975) *A classification of the biogeographical provinces of the world*. IUCN Occasional paper 18, World Conservation Union, Morges, Switzerland.
- Walsh, C. & Mac Nally, R. (2013) *hier.part: Hierarchical Partitioning. R package version 1.0-4*.