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

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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 geographical scale. In a multisite 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: Seventeen 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 specialization 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.

KEYWORDS

ecosystem function, ecosystem service, latitudinal gradient, longitudinal gradient, multisite experiments, Scarabaeidae

1 | INTRODUCTION

The ongoing loss of biodiversity highlights the importance of gaining insight into the relationship between species richness and ecosystem functioning (Duffy, Godwin, & Cardinale, 2017; Larsen, Williams, & Kremen, 2005). 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, Emberson, Krell, & Didham, 2014). Many studies highlight the importance of facilitation or niche complementarity and the value of multispecies assemblages for specific ecosystem functions (Cardinale,

Palmer, & Collins, 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 downscaled laboratory 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 geographical 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 (Doube, 1990). Another distinction can be made based on resource specialization 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 specialization 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, Lumaret, & Jay-Robert, 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, González-Megías, Jay-Robert, & Marqués-Ferrando, 2014). Functional group richness and species composition of dung beetle assemblages strongly affect key ecological functions such as dung removal and decomposition (O'Hea, Kirwan, & Finn, 2010), secondary dispersal of seeds already present in dung (Slade, Mann, Villanueva, & Lewis, 2007) and subsequent seed germination (D'hondt, Bossuyt, Hoffmann, & Bonte, 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, Wainwright, & Christie, 2015) such as nutrient cycling (Sitters, Maechler, Edwards, Suter, & Olde Venterink, 2014) and bioturbation (Brown, Scholtz, Janeau, Grellier, & Podwojewski, 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 as the 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 biogeographical regions across the Western Palaearctic. Here we asked the following questions: (a) How are dung beetle functional assemblages affected by "geography" (i.e., latitudinal and longitudinal trends) and climate variables?; (b) How does the relative abundance of resource specialists and generalists relate to geography?; and (c) 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.

2 | MATERIALS AND METHODS

2.1 | Study sites

We carried out a multisite experiment on 17 study sites across 10 countries in the Western Palaearctic realm (Figure 1a and Supporting Information Table S1). Each study site was assigned to a biogeographical region according to Udvardy (1975). The experiment was replicated both on a spatial scale by selecting study sites within the same biogeographical region (Supporting Information 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 (Supporting Information 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 2 years prior to the experiment.

2.2 | 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

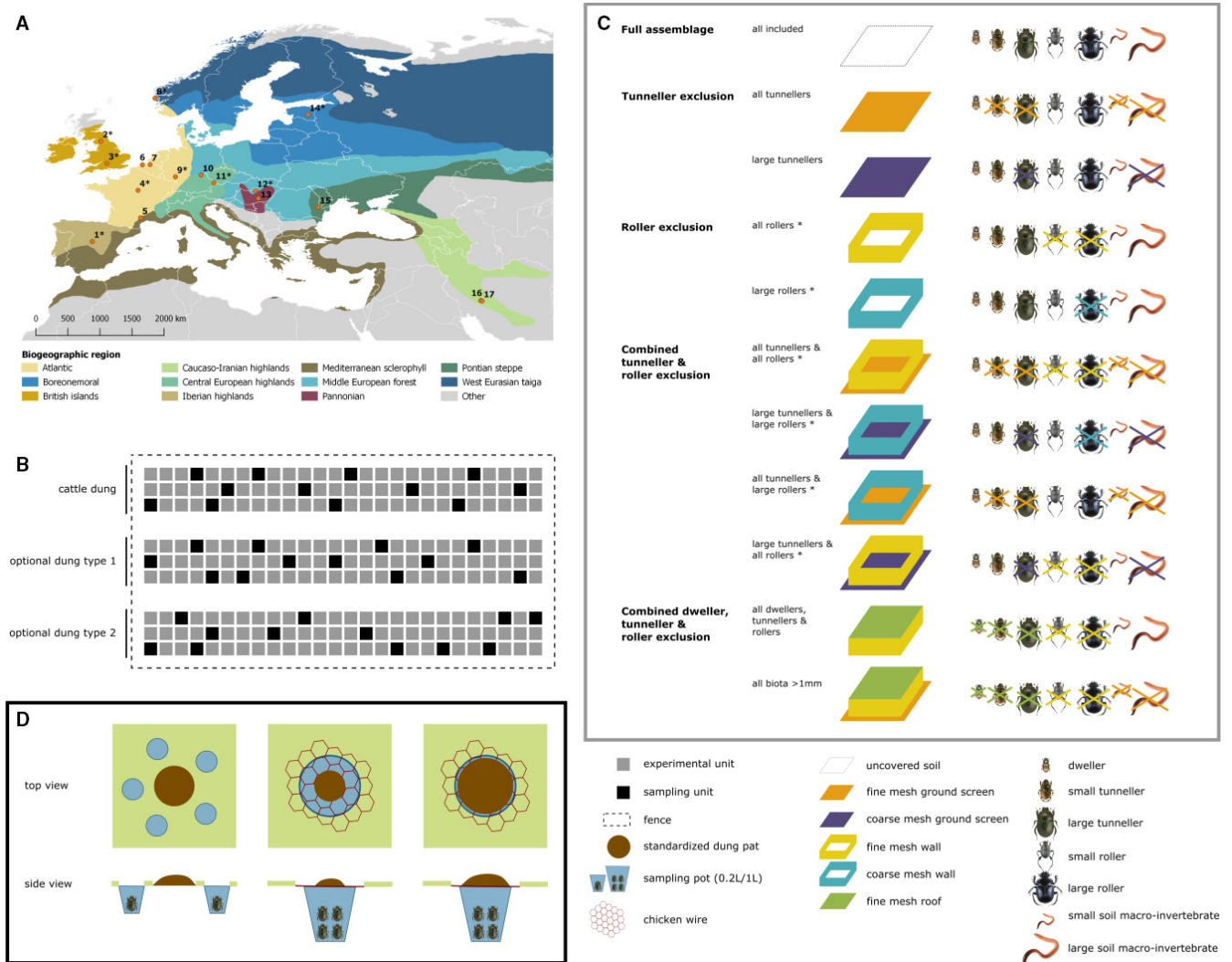


FIGURE 1 Setup of the multisite experiment estimating dung removal and secondary seed dispersal by dung beetles in the Western Palearctic. (a) Position of the study sites shown within biogeographical provinces as defined by Udvardy (1975); the digital base map was adapted from FAO Geonetwork (2015). See Supporting Information 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 two types of dung beetle sampling units. In the second year of the experiment sampling efforts were reduced with one sampling unit type in a similar setup. 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 centre of the plot, and functional groups were excluded using ground screens, walls and/or roofs made of fine (1 mm²) or coarse mesh (1 cm²). For each treatment, functional groups unable to move dung are crossed out. The colours of the crosses refer to the colours 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: five small pitfalls surrounding a central dung pile (left), and one large pitfall covered with a dung ball in a nylon bag (middle) used in the first year of the experiment, and one large pitfall covered with a large unpacked dung pile (right) used in the second year [Colour figure can be viewed at wileyonlinelibrary.com]

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 Palearctic dwellers are considered small species (D. Mann, per. commun.) 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, Giller, and Stakelum 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; Supporting Information Table S5).

2.3 | Experimental design

We designed 11 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-cm² mesh to exclude large individuals (while still including small individuals), and 1-mm² 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 five enclosure types was built at each site, while in areas where rolling species could occur six 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 setup 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).

2.4 | 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 6 weeks. This duration is considered long enough to suppress these attractive effects (Beynon, 2012).

Standardized amounts of dung (Supporting Information Table S3) were put in the centre of each experimental plot and left on site for 1 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:

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

In a subset of study sites, secondary seed dispersal by dung beetles was simultaneously measured during the dung removal

experiments. Therefore, 10 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} , Supporting Information 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, Quidé, Van Loo, and Hoffmann (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:

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

2.5 | 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 five 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 1 week after the start of the experiments. We emptied traps weekly for 3 weeks. For each dung beetle species sampled, we counted the total number of individuals per trap and sampling date.

2.6 | Data analysis

2.6.1 | 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 relationship 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.

2.6.2 | 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 data set. 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/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).

3 | RESULTS

3.1 | 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 sclerophyl 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 (Supporting Information 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 (Supporting Information 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 Supporting Information Table S7).

3.2 | 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

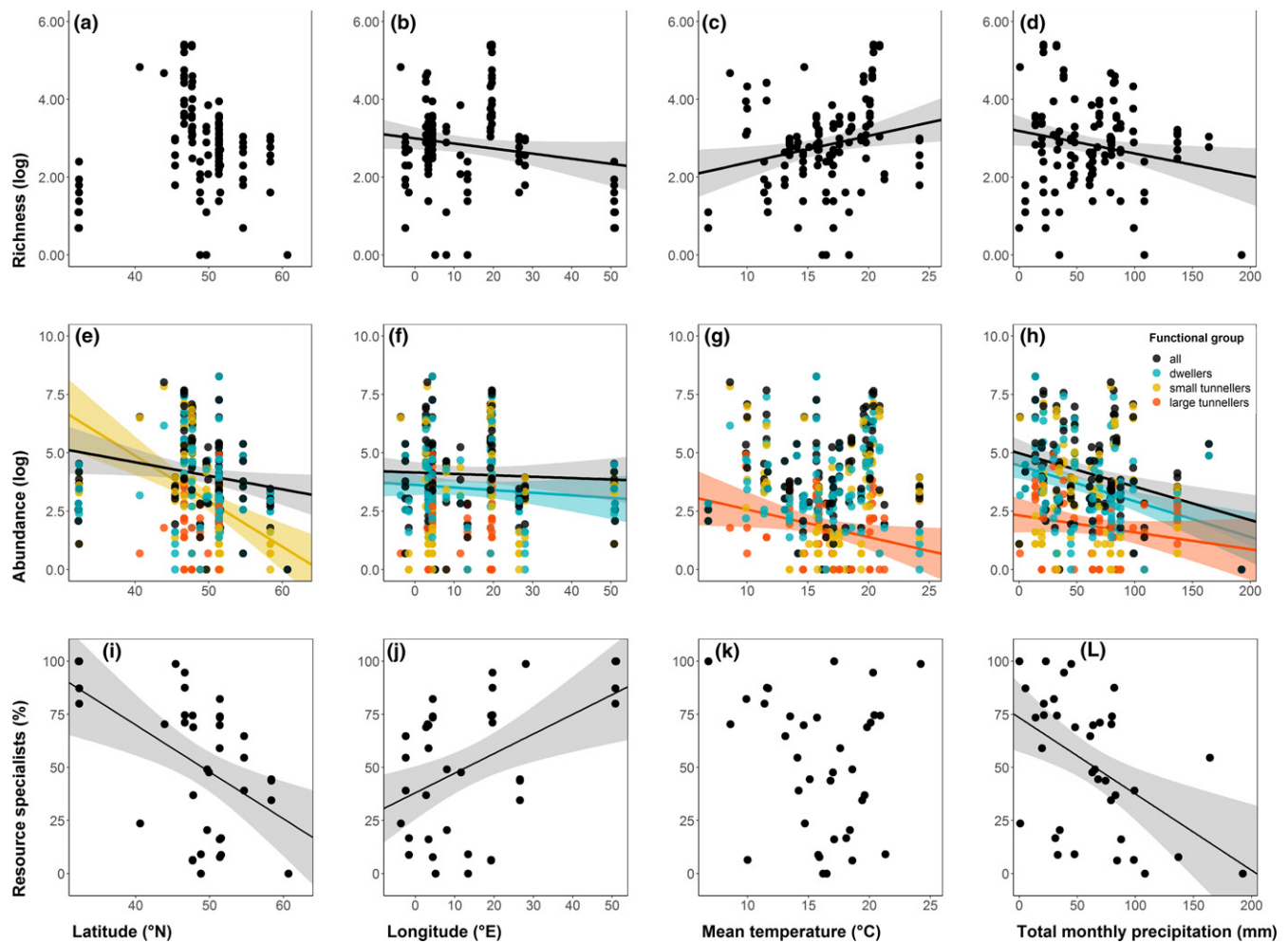


FIGURE 2 GLM model results showing relationships between species richness, dung beetle abundance or the proportion of resource specialist (y-axis) and latitude (a, e, i), longitude (b, f, j), mean temperature (c, g, k) and total monthly precipitation (d, h, l). Model-predicted means (solid lines) and standard errors are plotted for significantly correlated variables. Full model results are provided in Supporting Information Table S7 [Colour figure can be viewed at wileyonlinelibrary.com]

found strong positive correlations between secondary seed dispersal and dung removal in all studied biogeographical regions (Supporting Information Figure S1), although there were differences among seed sizes with a higher dispersal ratio for smaller seeds.

4 | DISCUSSION

4.1 | Functional composition

Northernmost regions were dominated by dwellers, while tunnellers and rollers become more prominent with decreased latitude. This corresponds well with the known biogeographical 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, Mazziotta, & Valerio, 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

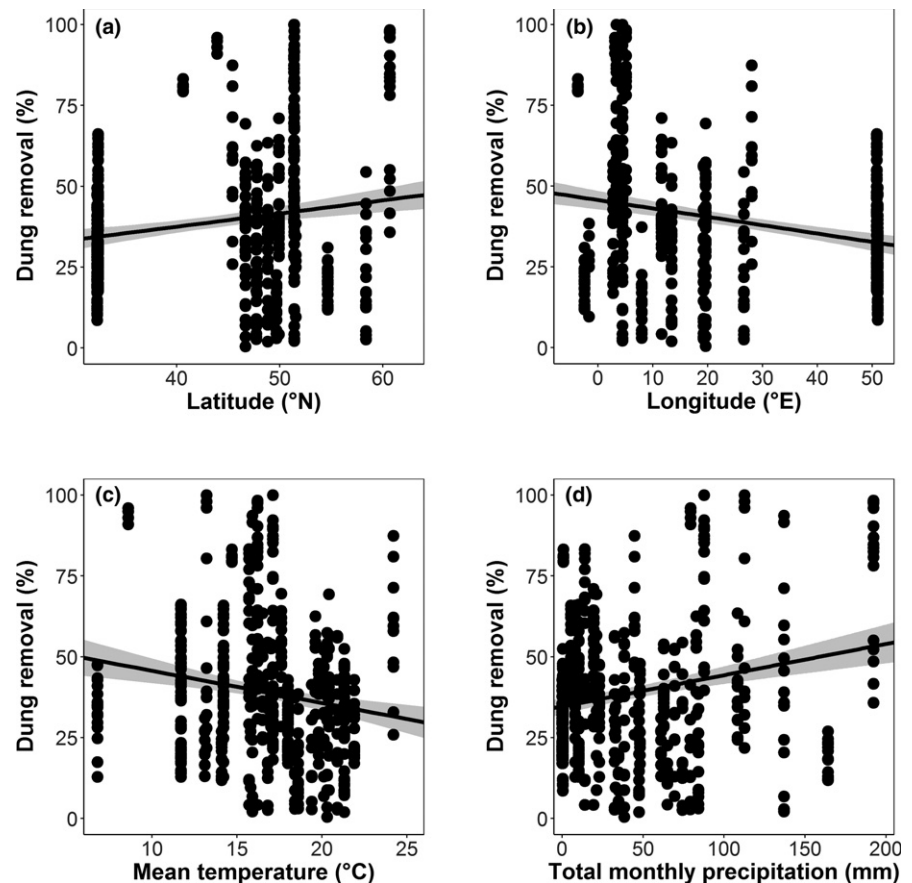


FIGURE 3 Dung removal in complete dung fauna assemblages in the Western Palearctic. Graphs show the relationship between the percentage of dung removed after 1 month and geographical (latitude (a), longitude (b)) and climatic variables (mean temperature (c), total monthly precipitation (d)). Significantly correlated variables after GLM analysis are plotted as solid lines with standard errors (grey). Full model results are provided in Supporting Information Table S8

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 Palearctic (Dortel et al., 2013).

4.2 | 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 colonized 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, Hardwick, & Roslin, 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

TABLE 1 Model results of the generalized linear models for dung removal and seed dispersal by dung beetles in the Western Palearctic. 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/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

Response variable	Predictor variable	t-value	p-value
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
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
	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

(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, Korasaki, Andresen, & Louzada, 2013). The high contribution of rolling

species in southern Europe also highlights the potential negative consequences of the ongoing decline in the abundance and diversity of roller species in this region for the ecosystem functions measured here (Carpaneto et al., 2007).

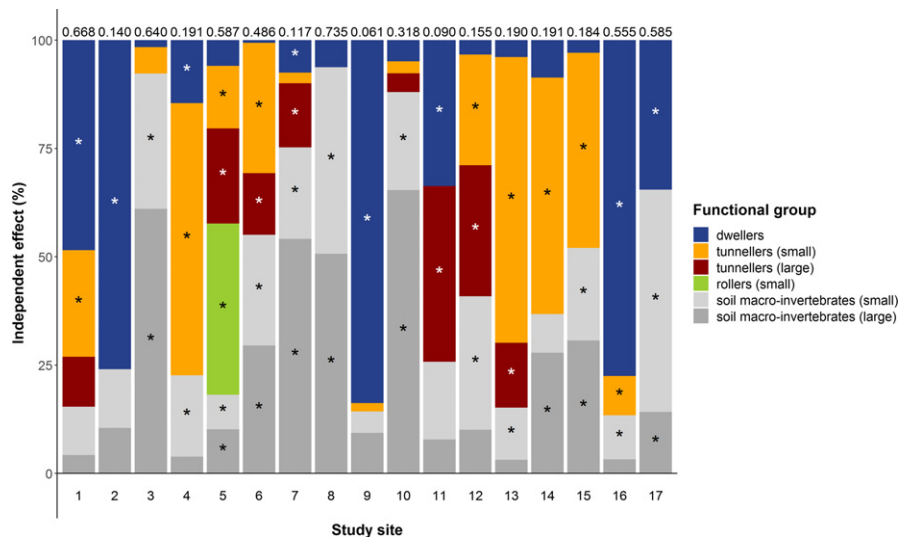


FIGURE 4 Hierarchical partitioning results for dung removal by dwellers, tunnellers, rollers and soil macro-invertebrates in the Western Palearctic. Displayed is the percentage of independent effect contributed by each functional group in each study site. Study sites are coded according to the codes in Figure 1 and Supporting Information 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 1,000 permutations. On top of each bar R^2 values of the total model is shown for each study site [Colour figure can be viewed at wileyonlinelibrary.com]

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 the 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 (Nichols et al., 2008; Shepherd & Chapman, 1998). 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, Azcárate, Peco, & Malo, 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, Slade, Beynon, & Lewis, 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.

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DATA ACCESSIBILITY

All data are available as open data. Dung beetle sampling data have been published as a sampling event data set 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>).

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BIOSKETCH

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.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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