ECOSYSTEM FUNCTIONS AND SERVICES PROVIDED BY DUNG BEETLES: A GLOBAL META-ANALYSIS

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Conflict of Interest

The authors have declared that there are no competing interests.

Abstract

Dung beetles are known to carry out a range of ecosystem functions such as secondary seed dispersal, bioturbation, nutrient cycling, plant growth, pest and parasite control, and trophic regulation, many of which support key ecosystem services. Despite the globally purported significance of this group of insects for ecosystem functioning, there has been no quantitative synthesis to establish the extent of dung beetle effects on ecosystem functions at global, regional, and habitat scales. To address this knowledge gap, we conducted a meta-analysis using 455 effect sizes collected from 66 published studies. The analyses evaluated the overall effects of dung beetles on 24 ecosystem functions, with additional subgroup analyses investigating (i) variation in dung beetle nesting behaviour, (ii) ecosystem type, and (iii) study methodology. Trophic regulation was found to be the ecosystem function most strongly enhanced by dung beetles, followed by nutrient cycling, plant growth enhancement, dung removal, bioturbation, and secondary seed dispersal. However, our analysis revealed considerable biases across the type of function assessed, with a significant focus on dung removal (57% of measured ecosystem functions) compared to nutrient cycling (20%) and less focus on other processes such as bioturbation, secondary seed dispersal, plant growth enhancement, and trophic regulation (<10%). our findings confirm that dung beetles have a net positive effect on multiple ecosystem functions, but with uneven distribution in the measurement of these functions across countries and latitudes, which could potentially lead to biased estimates of the impact of dung beetles on ecosystem functioning. These results emphasize the importance of quantifying a range of ecosystem functions beyond just dung removal, so as to gain a better understanding of the effects of dung beetles on multiple ecosystem services. By explicitly measuring multiple ecosystem functions, future ecological research on dung beetles will better describe the global contributions of dung beetle biodiversity to ecosystems and people.

Key words

Insectageddon, quantitative evidence synthesis, ecology, effect size, Scarabaeinae, geographic distribution, biodiversity, dung removal

Introduction

The stability and functioning of ecosystems occurs through the complex interaction of species, leading to beneficial processes enhancing nature's contributions to people (Díaz et al., 2018). Insects are of great significance in maintaining fundamental ecological processes that underpin ecosystem functioning, such as enhancing decomposition, nutrient cycling, and plant productivity (Hartley & Jones, 2008), facilitating seed dispersal (Chen et al., 2017), and regulating harmful parasite populations (Sands & Wall, 2017). However, the intensification of land use and changing climate patterns are posing increasing pressures on these insect communities and their capacity to contribute to ecosystem functioning (Outhwaite et al., 2022). Furthermore, our current understanding of the ecosystem services provided by insects is still limited and often biased, with significant gaps in knowledge regarding the least-studied functional and taxonomic groups (Noriega et al., 2018). There are potentially concerning negative trends in biodiversity and population abundance among insects, surpassing the rates observed compared with other taxonomic groups (Van Klink et al., 2020). This so-called “insectageddon” has raised significant concerns about the future functioning and stability of ecosystems (Cardoso et al., 2020; Eggleton, 2020; Thomas et al., 2019).

Dung beetles (Coleoptera: Scarabaeoidea) are a functionally significant group of insects due to their utilisation of dung to feed and protect offspring. This behaviour has cascading effects on ecosystem functions such as bioturbation, nutrient cycling, decomposition, and plant growth enhancement. These functions are vital to the stability and resilience of ecosystems (Nichols et al., 2008). The decline in insect biodiversity and biomass at large is mirrored in reports specifically on dung beetle communities, with dung removal, soil excavation and seed dispersal having been shown to decline with forest degradation, which has been attributed to decreased dung beetle biomass (López-Bedoya et al., 2022). In tropical regions, habitat fragmentation has led to large vertebrate defaunation. This has had cascading negative effects on associated dung beetle communities and ecological processes they drive (Andresen & Laurance, 2007; Nichols et al., 2009; Raine & Slade, 2019). Similarly, Bogoni et al. (2019) found that, alongside environmental factors such as climate and vegetation, decreases in diversity of medium- to large-bodied mammals in the South American Atlantic Forest biome seemingly led to a reduction in dung beetle species richness. In temperate regions, decline of telecoprid dung beetles from the Iberian Peninsula has been observed in areas with increased urban development since 1950 (Lobo, 2001) and in Italy, populations of telecoprid dung beetles have changed over the course of the 20th century, with nine species experiencing a decline in the past 30 years, also linked with changes in land use (Carpaneto et al., 2007). Overall, these trends threaten the essential ecosystem functions and ecosystem services that dung beetles provide (Noriega et al. 2021).

Nesting behaviour is one major factor contributing to the variation of ecosystem functions delivered by dung beetles (Halffter & Edmonds, 1982). This behaviour has been classified into four groups including non-nesters, telecoprids, paracoprids, and endocoprids (Tonelli, 2021). These nesting groups are often recorded and analysed as functional traits, due to the different strategies used for dung re-location, which can have strong effects on the level of ecosystem function delivered (deCastro-Arrazola et al., 2022). For example tunnelling and rolling behaviour can enhance dung removal by nearly 50% and have cascading ecological implications for the secondary dispersal of seeds (with reported increases by over 30%; Milotić et al. 2019). For this reason, paracoprid species are often selected for introduction programmes to novel environments, as they have been shown to redistribute dung that would otherwise remain on the pasture surface (Doube et al., 2014c). While many studies quantify the effects of different nesting strategies on ecosystem functions (Hea et al., 2005), our understanding of the overall magnitude and direction of effects of dung beetles and their nesting strategies on ecosystem functions is still limited.

Greater biodiversity of dung beetles can increase rates of ecosystem functioning (Noriega et al., 2021b) and it has been shown that dung beetle specialisation and preference for dung resources varies across regions along the latitudinal gradient, with greater diversity of beetles using dung resources to a greater extent at the equator (Frank et al., 2018). However, the landscape type can affect this considerably. For example, production landscapes such as agricultural fields and pastures are often more homogenous and the use of livestock pharmaceutical products and other agricultural chemicals can result in negative impacts on dung beetle populations and their ecosystem functions (Manning, Slade, et al., 2017; Verdú et al., 2018). In contrast, wild, intact ecosystems such as native forests and grasslands, typically have more abundant and diverse dung beetle assemblages, and have been found to have greater rates ecosystem functioning (Braga et al., 2013). There are unique dung beetle communities in different habitats, such as desert (deCastro-Arrazola et al., 2018) and grassland systems (Evans et al., 2019), which likely also modulate the net functional effects of dung beetle communities due to species-specific effects. Nevertheless, there is still a fundamental lack of any comparative overview of the magnitude and direction of how ecosystem functioning varies across these inherently variable features of native ecosystems.

With the increasing encroachment of livestock farming into new land areas, the ecology of dung beetles has become a matter of considerable economic concern and ecological significance (Doube et al., 2014), as novel dung beetles are increasingly being introduced to cattle-breeding areas that lack efficient native species that provide critical ecosystem services (Dymock, 1993; Forgie et al., 2018). However, it remains unclear whether dung beetle assemblages introduced to agricultural environments are as functionally effective as when in their native home range because there has been no comparison between the introduced versus native dung beetles and their impact on ecosystem functions. While laboratory studies can provide insights into the mechanisms underlying dung beetle-mediated ecosystem functions (Ortega-Martínez et al., 2016), they can also limit the generalisability of their outcomes to native ecosystems. In contrast, field studies can provide a more realistic assessment of the ecological impacts of the beetles under investigation; for instance field mesocosm experiments that measure rates of dung removal have been shown to be a reliable method for studying ecological impacts *in situ* (Lähteenmäki et al., 2015). Experimental studies aim to establish cause-and-effect relationships by manipulating variables in a controlled setting. However, patterns of dung beetle activity, such as abundance, diversity, and behaviour, identified through observational studies may reveal different patterns of variation in ecosystem functions delivered. As a consequence, there may be variations in outcomes between observational studies and experimental studies when evaluating the effects of dung beetles on ecosystem functions. There is also currently a lack of studies that compare these different methods and assess how they influence our understanding of the effect of dung beetles on ecosystem functions.

In a seminal, qualitative literature review, Nichols et al. (2008) inspired numerous studies investigating the effects of dung beetles on ecosystem functioning. A subset of ecological effects of dung beetles have been investigated using meta-analytical methods. For example, the study conducted by Nichols et al. (2007) found a reduction in dung beetle communities as a consequence of land use change in tropical regions. Similarly, López-Bedoya et al., (2022) reported adverse impacts of forest degradation and deforestation on the essential roles of dung beetles, including dung removal and seed dispersal. In contrast, Fuzessy et al., (2021) showed that the loss of habitat and depletion of large mammals have detrimental effects on dung beetle populations and their associated ecosystem functions. Collectively, these examples underscore the absence of a comprehensive quantitative synthesis of global patterns of dung beetle effects on various ecosystem functions and services.

Here, we investigate dung beetle contributions to ecosystem functioning, and the factors that affect the magnitude and direction of these effects through a meta-analysis approach which includes dung beetle nesting behaviour, ecosystem type, and study methodology. We hypothesise that (1) dung beetles will have an overall positive effect on ecosystem functions and paracoprid (tunnelling) behaviour will show the greatest rates of ecosystem functioning; (2) there will be greater ecosystem function delivery at tropical latitudes, intact landscapes and native habitats; and finally (3) there will be no difference between native versus non-native (introduced) dung beetles on ecosystem functioning, and there will be no difference in the level of ecosystem functions in laboratory versus field, and observational versus experimental studies.

Methods

Literature search

I used an automated approach to identify search terms that were considered relevant to our overarching question using the ‘litsearchr’ package (v 0.1.0) in R (Grames et al., 2019). Following this standardised systematic literature search framework, we conducted a naïve search using search terms that we considered relevant to our overarching question: what are the effects of dung beetles on ecosystem functions? We used the following Boolean search string:

dung beetle* AND ecosystem* AND function*

No restriction was placed on publication year, and this process returned a total of 378 unique papers from the Web of Science and Scopus databases (Appendix 2.1). To capture more papers for our meta-analysis, we used a systematic text mining exercise of paper titles, abstracts, and keywords, and generated a list of dung beetle stop words (n = 186) (Appendix 2.2) by manually assessing each word and combining with the standard English stop words. We obtained a pool of 1271 search terms and, to understand their relatedness based on their co-occurrence in papers, we generated a feature matrix and visualized word association networks (Appendix 2.3). By detecting commonly appearing terms, we was able to identify important nodes, which allowed me to select 92 key terms, which were then grouped into concept groups following the PICO framework (Appendix 2.1). The automated Boolean search string was:

> \(\(“dung fauna” OR beetle OR biomass OR coleoptera OR “dung beetle” OR “functional group” OR insect OR scarabaeidae OR scarabaeinae OR species\) AND \(manure OR cattle OR dung OR livestock OR mammal\) AND \(“primary productivity” OR “carbon sequestration” OR bioturbation OR “seed dispersal” OR “plant growth” OR “secondary seed dispersal” OR “parasite control” OR “fly control” OR “trophic regulation” OR pollination OR decomposition OR dispersal OR “dung removal” OR feeding OR interaction OR “nutrient cycling” OR pasture OR soil OR vegetation\) AND \(abundance OR biodiversity OR conservation OR disturbance OR diversity OR ecological OR ecology OR ecosystem OR functional OR functions OR richness OR “species composition” OR “species richness”\)\)

Using this returned 30,292 papers on WOS and 20,907 papers on SCOPUS. After a first assessment of the search terms suggested by the automated Boolean search string (above), we decided that this cast the net too wide. Thus, based on combined knowledge of the dung beetle ecology literature and assessment of the naïve search, we decided to use the naïve search terms (above) for the final search, as this captured a good sample size and subset from the larger automated search of the most relevant studies for this research question. However, the automated key term search proved to be a beneficial exercise, as it revealed that while the dung beetle ecology literature may briefly mention terms such as “ecosystem functions” or “ecosystem services,” these terms are not reiterated in the abstract or implemented as part of the study design. Instead, the potential outcomes of ecosystem functions and underlying biotic or abiotic mechanisms are described as discussion points and potential outcomes, without explicit measuring and analysis of ecosystem functions.

Abstract and article screening

I assigned each article a unique study ID, and then conducted an abstract screening by reading abstracts using the ‘Metagear’ package (Lajeunesse, 2016). We ensured that the following criteria were met to choose studies for analysis, including (i) explicit quantification of dung beetle-mediated ecosystem functions; and (ii) the reporting of mean values of variables, sample size, and a measure of variability around the mean. In cases where multiple habitats, species, or response variables were examined separately within the same article, we treated them as distinct case studies since they were considered independent. Finally, for response variables that were measured at multiple time points, we included each time point in the analysis and where studies measured responses across seasons, we included each season in our analysis. Abstracts were screened three times to ensure that no papers were missed. Interestingly, many papers stated that they had control treatments, but did not report control treatments in the text, figures or supplementary materials, which created a final sample size of 66 studies (Appendix 2.1).

Data extraction

For each study, we coded details of the article ID, geographic location, environmental variables, and study methodology. We extracted 24 dung beetle associated ecosystem functions by recording means, measures of variability and sample sizes for each response variable from the control (dung beetles absent) and the treatment (dung beetles present) and then re-codified these ecosystem functions by grouping them according to the groups of functions described in Nichols et al. (2008) (Table 2.1). In articles where data were not reported in the text or supplement, we extracted data using the image analysis graphical user interface ‘WebPlotDigitizer’ V 4.6 (Rohatgi, 2022). To investigate our hypotheses using subgroup analysis, we coded nesting behaviour, ecosystem type, and study methodology factors as categorical variables in the database (Table 2.2).

Effect size calculations

All analyses were done using the ‘metafor’ package in R version 4.2.2 (Viechtbauer, 2015). We used Hedges’ g to calculate standardised mean differences as a measure of treatment effect sizes. Hedges’ g takes into account sample size and the inverse of variance, thus correcting for positive bias in standardised mean differences inherent in the Cohen's D value. (Viechtbauer, 2010). This standardised value has a range from $-\infty$ to $+\infty$, where negative and positive values indicate either an increase or decrease in ecosystem functions (respectively), resulting from the presence of dung beetles. A larger effect size implies a more pronounced difference between the experimental control (no dung beetles present) and treatment (dung beetles present), while a Hedges’ g of zero suggests no difference in the examined response variables across treatments.

Random effects meta-analysis and subgroup analyses

I first ran a random effects meta-analysis using all individual ecosystem function effect sizes combined to test for overall differences in ecosystem functions between study controls (no dung beetles) and treatments (with dung beetles), hereafter displayed as $Q_{overall}$. we then grouped data into each ecosystem function category to test responses of each function separately (Table 2.1). To assess the variability of dung beetle-mediated ecosystem functioning across different dung beetle nesting behaviours, ecosystem types and study methodologies, separate random effects meta-analyses were performed for each sub-group (Table 2.2) using the restricted maximum-likelihood estimator (Viechtbauer, 2010). To test the difference ($Q_{difference}$) between each sub group, we used a random effects meta-analysis, yielding estimates of heterogeneity (I^2) and Q-test of heterogeneity (Q) (Viechtbauer, 2010). Moderator levels with less than four cases are not informative enough and should be interpreted with caution due to their potential unreliability. Despite being aware of the limitations of including ecosystem functions with less than four effect sizes, we made a deliberate choice to include them in the effect displays to explore and highlight the extent of knowledge gaps.

Publication bias

Publication bias is a major limitation of evidence synthesis and meta-analytic research (Osenberg et al., 1999). While we took the appropriate precautions against this at the start of our research (using ‘litsearchr’ and multiple abstract screenings), we also conducted *post-hoc* tests of publication bias by producing funnel plots to assess any asymmetry (also using the ‘metafor’ package in R). A funnel plot is expected to have a symmetrical inverted funnel shape when there is no publication bias, with the smaller studies scattered randomly around the effect size estimate, and more extensive studies clustered more tightly around the “true” effect size. However, if publication bias is present, the funnel plot may show asymmetry, where the smaller studies with fewer significant or no effects are missing, resulting in an asymmetrical plot (Viechtbauer, 2010). To assess funnel plot asymmetry, the rank correlation test and the regression test were performed, using the standard error of the observed outcomes as a predictor (Appendix 2.5). The field of ecology is greatly impacted by the “file drawer problem”, which refers to a bias towards publishing statistically significant results while neglecting non-significant ones (Rosenthal, 1979). Consequently, a considerable number of effect sizes reporting on ecosystem functions mediated by dung beetles may remain unpublished and as a result are not able to be included here.

Table 0.1 Categories given to ecosystem function effect sizes extracted from the literature following Nichols et al (2008)

Ecosystem Function	Example measured variables from published literature
Dung removal	Dry mass dung removed/remaining on the surface Wet mass dung removed/remaining on the surface
Nutrient cycling	Ammonium N Leachate N Leachate P Microbial respiration Moisture Nitrogen Organic matter Potassium Total carbon Total nitrogen Total phosphorus
Bioturbation	Bulk density
Plant growth enhancement	Foliar nitrogen Foliar phosphorus Number of seedlings Leaf number
Secondary seed dispersal	Seed mimic size (small, medium, large) Burial depth Distance of seed mimic from dung
Pest / parasite control	Adult fly abundance Fly larvae abundance E. coli colony count
Trophic regulation	Bait strip consumption

Table 0.2 Variables that were codified at the study level that could explain variation in the effects of dung beetle presence on measured ecosystem functions

	Study-level factor	Subgroup
Functional trait	Nesting behaviour	Paracoprid Endocoprid Telecoprid Mixed
Ecosystem type	Latitude	Temperate Tropical
	Landscape	Production Wild
	Habitat	Agriculture Desert Forest Grassland
Methodological factors	Dung beetle status	Introduced Native
	Study context	Laboratory Field
	Study method	Observational Experimental

Results

Database characteristics

After screening the literature and applying the aforementioned selection criteria to screened studies, the resulting dataset comprised 455 effect sizes extracted from 66 peer-reviewed papers (Appendix 2.1), with a notably uneven distribution across countries (Figure 2.1; Appendix 2.6). Dung removal accounted for 57% of effect sizes, nutrient cycling for 20%, bioturbation for 5%, plant growth enhancement for 6%, secondary seed dispersal for 8%, and trophic regulation for 5% (Figure 2.2). The distribution of published effect sizes varied significantly across different geographic regions. Specifically, studies conducted in Brazil contributed the highest number of effect sizes to our analyses on dung removal (n = 39), bioturbation (n = 8), and secondary seed dispersal (n = 13). In contrast, studies from China provided the most effect sizes for nutrient cycling (n = 18), while those conducted in Mexico contributed the most to our analyses on plant growth enhancement (n = 11). Notably, trophic regulation was only reported in studies conducted in the UK, with a total of 23 effect sizes included in our analyses. Further details on the regional distribution of effect sizes are in Figure 2.1 and Appendix 2.6.

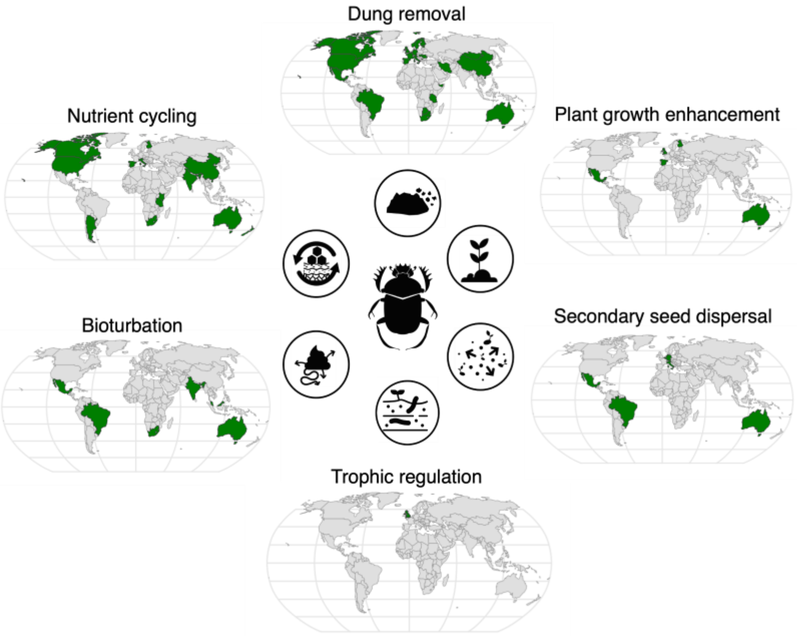

Figure 0.1 The global distribution of effect sizes extracted for each ecosystem function. See Appendix 2.6 for further information regarding individual countries.

Dung beetles enhance overall ecosystem functioning

The aim of this meta-analysis was to quantitatively examine the effect of dung beetles on ecosystem functions, based on published literature to date. We analysed seven ecosystem functions (Table 2.1), six of which had sufficient data for sub-group analysis with 18 moderators (Table 2.2). The results of our analysis show that dung beetles have a positive overall effect on all ecosystem functions reported here (Figure 2.2) Additionally, we found that dung beetle effects on four out of six functions varied significantly depending on nesting behaviour, with no effects of nesting behaviour detected for secondary seed dispersal (Figure 2.2e; Appendix 2.7) and trophic regulation (Figure 2.2f; Appendix 2.7).

The strongest effects of dung beetles on ecosystem functions were found for trophic regulation (Figure 2.2f; Appendix 2.7). This was followed by nutrient cycling (Figure 2.2b; Appendix 2.7), where endocoprid dung beetles contributed significantly to the enhancement of nutrient cycling (Figure 2.2b; Appendix 2.7). Although there was only a marginally significant difference in dung beetle effects between different nesting behaviours on plant growth enhancement, these results provide some indication that a greater level of plant growth enhancement may occur with mixed dung beetle nesting behaviours (Figure 2.2d; Appendix 2.7). Overall, we observed that mixed nesting behaviours had the most pronounced effect on dung removal (Figure 2.2a; Appendix 2.7). With 20 effects found in the literature, bioturbation showed significantly greater effects in studies with telecoprid dung beetles (Figure 2.2c; Appendix 2.7), however this should be viewed with caution since subgroup analyses were based on only three effect sizes (two paracoprids and one telecoprid effect size). Out of all functions quantified in the literature, secondary seed dispersal had the weakest response to dung beetle presence, and there was no difference in secondary seed dispersal between paracoprid and mixed nesting behaviours (Figure 2.2e; Appendix 2.7). Finally, we was unable to conduct any sub-group analyses for pest/parasite control due to insufficient data, so this function was not included in our analyses.

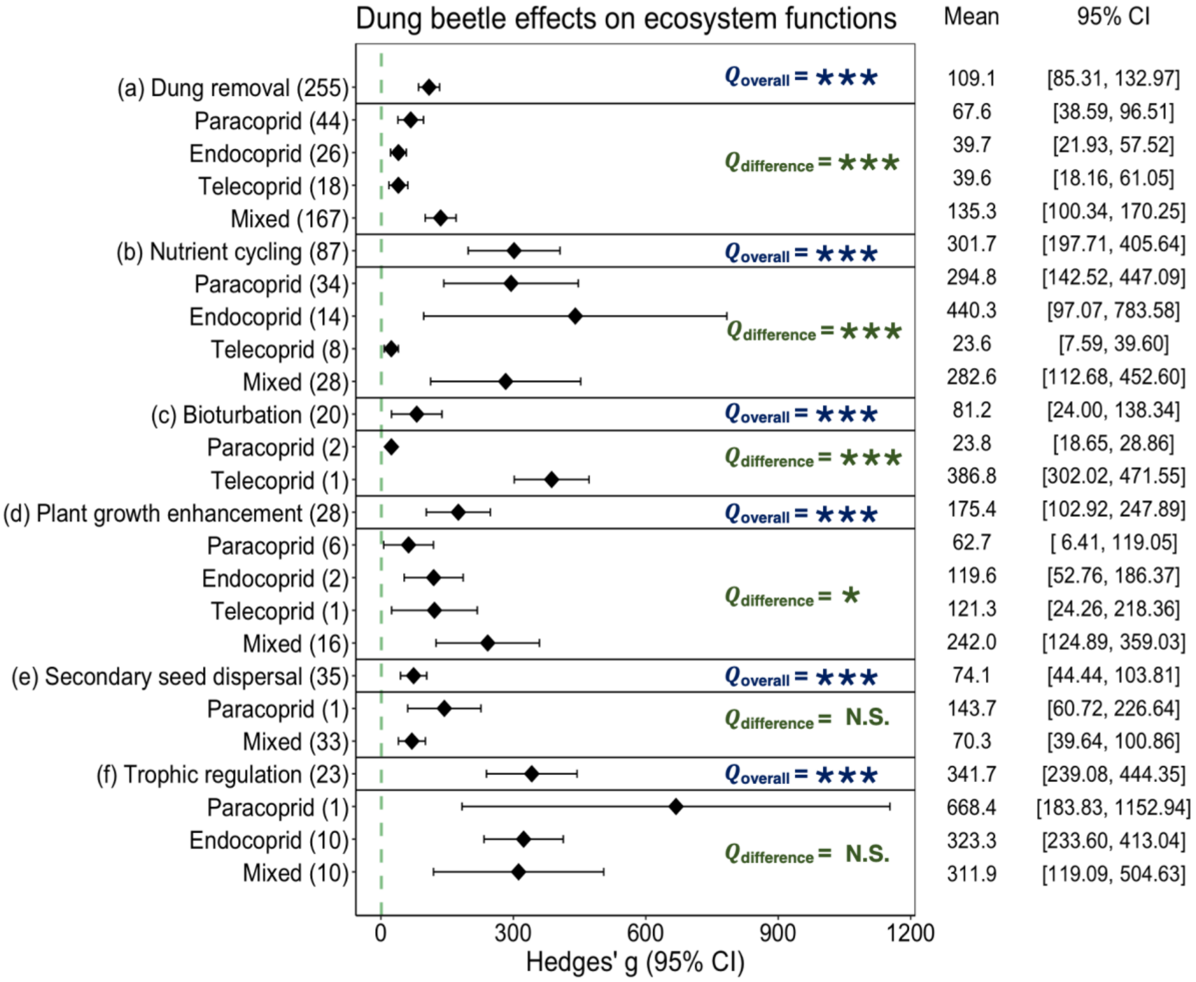

Figure 0.2 Global effects of dung beetles on all ecosystem functions reported in the literature. Hedges' g effect sizes +/- 95% confidence intervals are shown for (a) dung removal, (b) nutrient cycling, (c) bioturbation, (d) plant growth enhancement, (e) secondary seed dispersal, and (f) trophic regulation. Sub-group analyses further differentiate the influence of dung beetle nesting behaviour on each ecosystem function, which includes four categories: paracoprids (tunnelers), endocoprids (dwellers), telecoprids (rollers), and mixed (studies with two or more nesting behaviours). Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05.

Dung removal

There were significant differences in dung removal between temperate and tropical ecosystems, with a more substantial effect on dung removal observed in temperate ecosystems (Figure 2.3; Appendix 2.8). Similarly, a significant difference in dung removal was observed between production and wild landscapes, with production landscapes exhibiting a stronger effect on dung removal (Figure 2.3; Appendix 2.8). Dung removal varied significantly across distinct habitat types, with the effects of dung beetles on dung removal being most pronounced in grassland ecosystems, followed by deserts and agricultural lands, while forests displayed the weakest effect (Figure 2.3; Appendix 2.8). In comparison to introduced species, native beetles demonstrated a higher level of dung removal (Figure 2.3; Appendix 2.8). Observational studies exhibited a more substantial impact on dung removal than experimental studies, while there was no statistically-significant difference between laboratory and field studies (Figure 2.3; Appendix 2.8). Similarly, no statistically-significant difference in dung removal was observed between laboratory and field studies (Figure 2.3; Appendix 2.8).

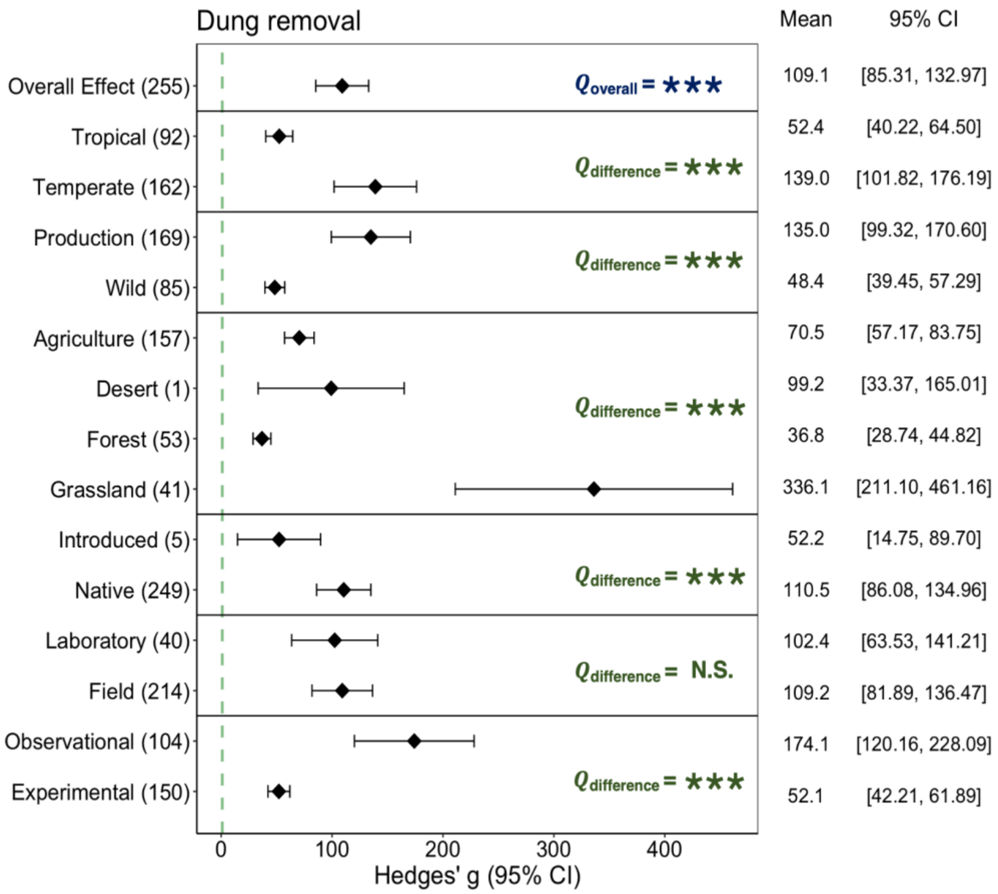

Figure 0.3 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in dung removal by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) introduced versus native dung beetles; (e) laboratory versus field studies; and (f) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05.

Nutrient cycling

The effect of dung beetle presence on nutrient cycling was significantly more pronounced in temperate ecosystems when compared to tropical ecosystems (Figure 2.4; Appendix 2.9). In comparison to wild landscapes, production landscapes showed a significantly lower degree of nutrient cycling (Figure 2.4; Appendix 2.9). Grassland habitats exhibited greater nutrient cycling facilitated by dung beetle presence and, surprisingly, the lowest nutrient cycling rates were observed in forest habitat (Figure 2.4; Appendix 2.9). There was no significant difference in nutrient cycling between introduced versus native dung beetles (Figure 2.4; Appendix 2.9). This was also the case for dung beetle effects on nutrient cycling between laboratory and field studies (Figure 2.4; Appendix 2.9), though the number of effect sizes for laboratory (n = 3) and observational (n = 1) studies were low and should be interpreted with caution.. However, there was a significant difference between observational and experimental studies, with higher nutrient cycling effects detected in experimental settings (Figure 2.4; Appendix 2.9).

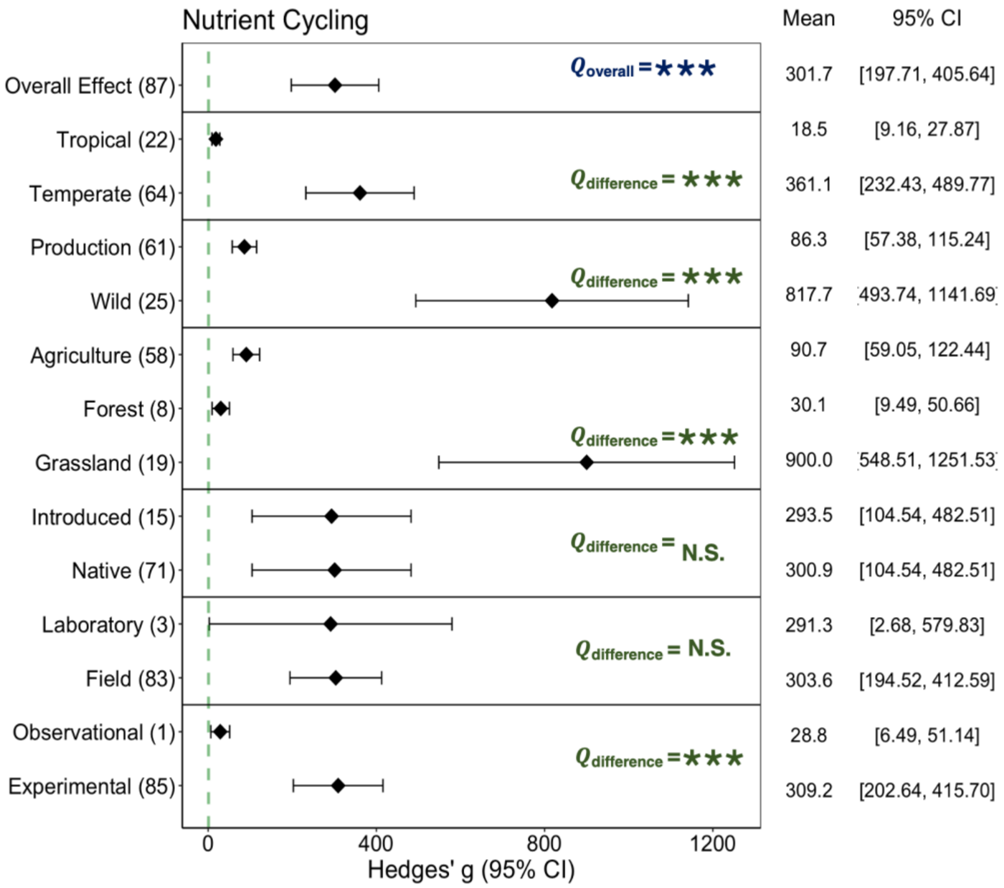

Figure 0.4 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in nutrient cycling by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) introduced versus native dung beetles; (e) laboratory versus field studies; and (f) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05

Bioturbation

I found that there was a greater level of bioturbation in temperate than in the tropical ecosystems, which did not support our initial hypothesis (Figure 2.5; Appendix 2.10). A significantly-higher amount of dung beetle-mediated bioturbation was found in production landscapes compared to wild, and there was no significant difference in bioturbation between habitat types (Figure 2.5; Appendix 2.10). Field studies also showed a higher level of dung beetle bioturbation compared to laboratory studies (Figure 2.5; Appendix 2.10), but there was no significant difference in effect sizes between observational and experimental studies (Figure 2.5; Appendix 2.10). We did not find any studies that quantified introduced versus native dung beetle mediated bioturbation, so this factor could not be tested in this meta-analysis. It is noteworthy that there were small sample sizes of the temperate, grassland and laboratory subgroups, which should be taken into consideration in interpreting the outcomes of these analyses (Figure 2.5; Appendix 2.10).

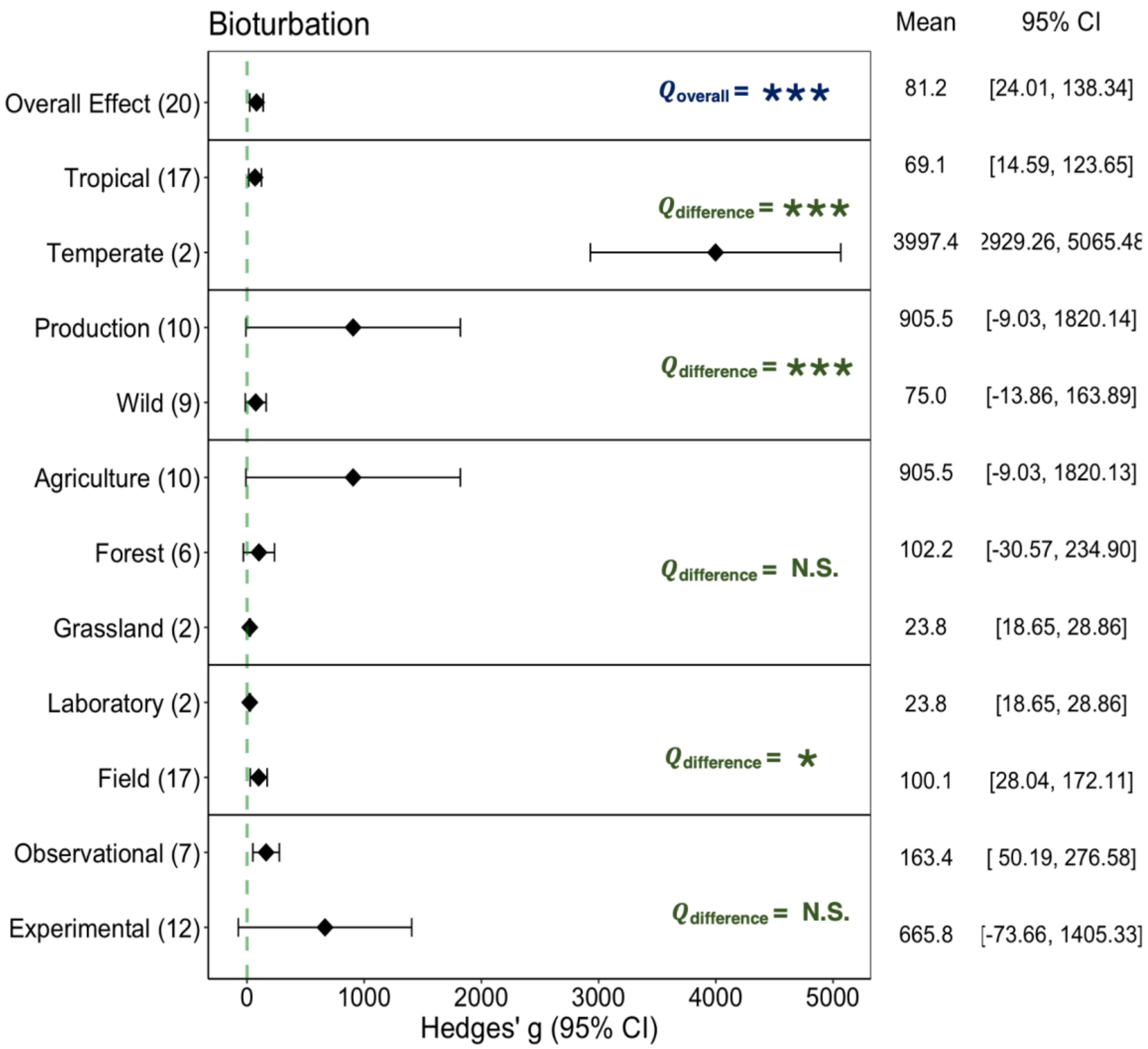

Figure 0.5 Hedges’ g effect sizes +/- 95% confidence intervals, illustrating variation in bioturbation by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) laboratory versus field studies; and (e) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05

Plant growth enhancement

My initial hypothesis was that dung beetles would show greater plant growth enhancement on tropical systems in contrast with temperate zones. Interestingly, we found that dung beetles had a positive effect on plant growth enhancement with no difference between both tropical and temperate ecosystems (Figure 2.6; Appendix 2.11). In the same way, dung beetles had similar effects on plant growth enhancement in both production and wild landscapes (Figure 2.6; Appendix 2.11) and there was no differences in dung beetle-mediated plant growth enhancement between agriculture and forest habitat types (Figure 2.6; Appendix 2.11). However, the effects of dung beetles on plant growth enhancement were significantly greater in studies with native dung beetles compared to introduced ones, which were slightly negative. It is important to note that the sample size for introduced species was only three, so these results should be interpreted with caution (Figure 2.6; Appendix 2.11). There was no significant difference in dung beetle mediated plant growth enhancement observed between the effect sizes of laboratory versus field studies and observational versus experimental studies (Figure 2.6; Appendix 2.11).

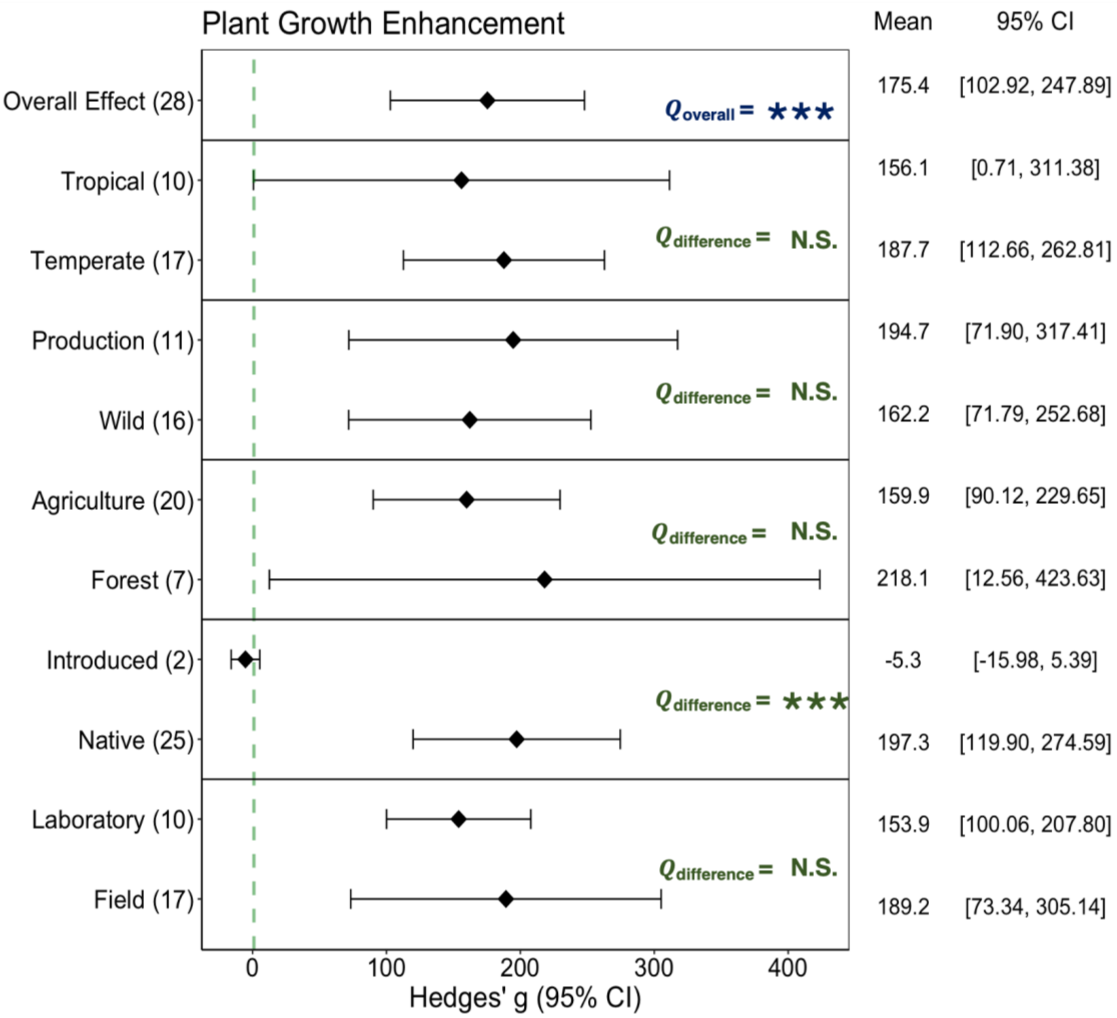

Figure 0.6 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in plant growth enhancement by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) introduced versus native dung beetles; and (e) laboratory versus field studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; N.S. $p > 0.05$.

Secondary seed dispersal

In contrast to all other ecosystem functions, secondary seed dispersal was significantly greater in tropical ecosystems compared to temperate ecosystems (Figure 2.7; Appendix 2.12). Dung beetles appear to deliver similar levels of seed dispersal in both production and wild landscapes (Figure 2.7; Appendix 2.12). Secondary seed dispersal mediated by dung beetles appeared to be greater in agricultural habitats compared to forest and grassland habitats, although the result was not statistically significant and may have been influenced by the small sample size of the grassland habitat (Figure 2.7; Appendix 2.12). There was no significant difference in the effects of dung beetles on secondary seed dispersal between laboratory and field studies. However, it should be noted that the laboratory subgroup had only one effect size, so this inference may not be reliable (Figure 2.7; Appendix 2.12). Finally, there was no significant difference in the effects of dung beetles on secondary seed dispersal between observational and experimental studies (Figure 2.7; Appendix 2.12).

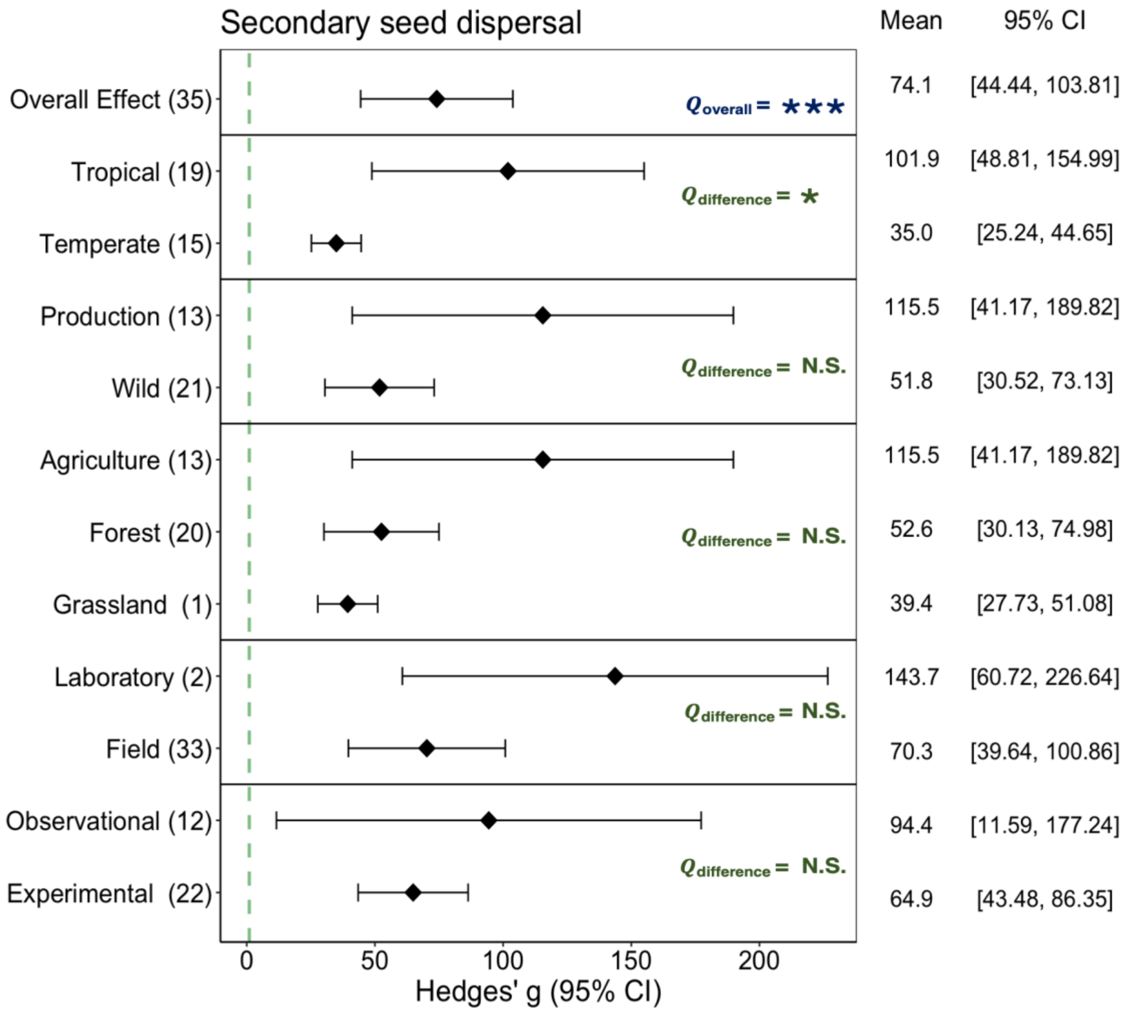

Figure 0.7 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in secondary seed dispersal by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) laboratory versus field studies; and (e) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05

Discussion

Dung beetles enhance all ecosystem functions studied

This meta-analysis is the first fully global, quantitative synthesis of dung beetle effects on ecosystem functions. The key outcomes of our study are (1) dung beetle presence has a positive effect on all measured ecosystem functions, with mixed or paracoprid nesting behaviours amplifying these effects (Figure 2.2); (2) contrary to our hypotheses, dung beetle mediated ecosystem functions were greater at temperate latitudes, production landscapes and grassland systems; and finally (3) introduced dung beetles had a slight negative effect on plant growth enhancement, and the magnitude of effect on ecosystem functions varied depending on whether the studies were conducted in the laboratory or field, as well as whether they were observational or experimental.

Differential effects of dung beetle nesting strategies on ecosystem functions

In contrast to our expectation, the presence of mixed dung beetle nesting behaviours resulted in greater dung removal and plant growth enhancement (Figure 2.2). This could be due to niche complementarity, where a diverse range of nesting behaviours allows for varying preferences for dung type, size, and location (Halffter & Edmonds, 1982). A diversified use of available resources can enhance dung removal and, in turn, plant growth (Menéndez et al., 2016). Further studies have shown that the presence of functionally contrasting dung beetles can have a synergistic, positive effect on soil microbial respiration and the decomposition rate of soil organic matter (Cheng et al., 2022), and can promote greater stability and resilience within the dung beetle community (Manning & Cutler, 2018a). This is beneficial for maintaining ecosystem functioning even under environmental disturbances or stressors (Mori, 2016). On the other hand, we observed a decrease in dung removal associated with telecoprid nesting behaviour, which may be attributed to inadequate experimental design in exploring such effects. For instance, Carvalho et al., (2018) suggested that their study on dung burial rates by telecoprid beetles might have used too much dung in the experiment, resulting in incomplete burial of the resource, thereby making it difficult to accurately determine the telecoprids' contribution to dung removal.

The results showed that nesting behaviour is an important trait to consider in dung beetle ecology research, as it could have important implications for decomposition processes. In a meta-analysis by McCary & Schmitz (2021), where they investigated the relationship between invertebrate functional traits and terrestrial nutrient cycling, they found that on a global scale, detritivores, and in particular bioturbators, promoted faster rates of decomposition as well as increased nitrogen pools. Furthermore, they found that decomposer invertebrates had greater predictive power when compared to herbivores or predatory feeding modes. Bioturbation is a key feature that enhances dung beetle decomposition, particularly with paracoprid dung beetles, as they mix organic matter into soil, increasing its surface area and exposure to microbes that can further break it down (Bertone et al., 2006). This highlights the importance of invertebrate functional traits in shaping ecosystem processes and the need to consider the diverse roles that different organisms play in nutrient cycling and decomposition, to best predict how these processes may vary under global change scenarios.

In contrast to our hypothesis, we found that paracoprids had the lowest effect on plant growth enhancement (Figure 2.2), which could be because of their tunnelling behaviour causing a large and rapid influx of dung and other detritus belowground, leading to high concentrations of nutrients at plant roots, which may affect root architecture and overwhelm growth in plants (López-Bucio et al., 2003; Xiao et al., 2020). The amount of time it takes to bury dung could affect subsequent ecosystem functioning, for example, Stanbrook et al. (2021) categorised dung beetles within communities in Tanzania based on their size and their burying speed, with the beetles being divided into fast-burying and slow-burying tunnellers of both large and small body sizes. The study found that the speed of dung burial affected ecosystem functions, with larger beetles moving more macronutrients into the soil given the same time period. Furthermore, the larger dung beetles moved more nitrogen, phosphorus, potassium, and carbon than smaller dung beetles. This demonstrates that plant growth enhancement could depend on the nesting behaviours and sizes of the dung beetle community over time.

In addition to this, our results showed that endocoprid behaviour enhanced nutrient cycling, possibly due to the slower rate of nutrient incorporation into the soil or microclimate and microhabitat conditions created around deposited dung on pasture, fostering a moist environment for an optimum rate of nutrient cycling (Sowig, 1995). While our results showed no difference between nesting behaviours for dung beetle effects on secondary seed dispersal and trophic regulation, this is likely because there were limited data to illustrate these effects. This underscores that there is a very large data gap in the field of dung beetle functional ecology.

Dung beetle effects on ecosystem functions across ecosystem types

Temperate latitudes showed significantly greater effects across dung removal, nutrient cycling, bioturbation, and plant growth enhancement. This was in contrast to our hypotheses, but there are several reasons that could support this outcome. In temperate climates, decomposition rates may be higher due to more pronounced seasonal changes in temperature (Duarte et al., 2016). Van Groenigen et al. (2014) found that earthworm presence showed decreased aboveground biomass in temperate compared to tropical climates, suggesting decomposition is greater in the temperate zone. Furthermore, they discuss implications for this in tropical climates, where decomposition rates may be higher due to the warm and humid conditions year-round, the presence of earthworms may not have as much of an impact on aboveground biomass. They conclude that this could be because the rate of decomposition is already high, and therefore, the contribution of earthworms to the decomposition process is relatively small.

In a meta-analysis by (López-Bedoya et al., 2022) investigating primary forest loss and degradation on dung beetle biodiversity, deforestation that occurred in temperate latitudes led to an increase in dung beetle species richness and no difference in species abundance. In contrast, they found that in tropical latitudes both dung beetle richness and abundance declined significantly under deforestation or degradation. We think this could be because temperate and tropical regions have different ecological characteristics and climatic variation, for example, temperate regions have variable resources due to seasonality, so there could be a lag time before negative effects are detected at different trophic levels (Krauss et al., 2010), when compared to tropical latitudes, which have more constant climatic conditions, which could mean specialised dung beetle species which could be more vulnerable to habitat loss. For example, Englmeier et al., (2022) found that community specialisation of dung-visiting beetles is driven by climate, while diversity is mainly affected by land use intensification.

Anthropogenic factors, such as agricultural practices, may play a role in shaping the latitudinal trends observed in dung beetle-mediated ecosystem functioning. Specifically, it is possible that agricultural landscapes provide greater dung resources for dung beetles due to greater stocking densities. However, while it has been shown that the amount of resource available and dung beetle abundances are related, the response of dung beetles to changes in the amount of resource available depends on the species and the structure of the landscape (Roslin & Koivunen, 2001). Alternatively, it is possible that the trends found in agricultural landscapes here are more related to human agricultural productivity practices (such as mulching) and not dung beetles alone.

The relative contributions to soil microorganism-mediated global nutrient cycling varies spatially. It has been found that soil bacterial genetic diversity is highest in temperate habitats, with fungi and bacteria showing global niche differentiation associated with contrasting diversity responses to precipitation and soil pH, which could be associated with dung decomposition patterns found in our meta-analysis (Bahram et al., 2018). However, further research is needed to fully understand the underlying mechanisms driving these latitudinal patterns of dung beetle effects on ecosystem functioning, as this pattern could be attributed to data gaps from tropical latitudes.

We found dung beetle mediated secondary seed dispersal is significantly higher in tropical latitudes (Figure 2.12). Tropical regions are characterized by high levels of biodiversity and a greater abundance of frugivorous animals and larger seeds that are easier to quantify, which may contribute to greater secondary seed dispersal in tropical ecosystems (Braga et al., 2017; Griffiths et al., 2016). It will therefore be important for future studies to quantify secondary removal of smaller seed sizes that are typically found at temperate latitudes, as dung beetles have been shown to potentially assist in ecological restoration by acting as secondary seed dispersers, potentially increasing the success of projects to restore areas with degraded soil and vegetation cover (Almeida et al., 2022).

Our study compared the effects of production and wild landscapes on dung removal, nutrient cycling, bioturbation, and plant growth enhancement. We found that production landscapes had the highest rates of dung removal and bioturbation, while wild landscapes exhibited the greatest nutrient cycling. Furthermore, although plant growth enhancement was greater in production landscapes, the effect was not statistically significant. These landscape-scale findings provide valuable insights into the trade-offs and benefits of different types of landscapes for ecosystem functioning.

Effects of study methodology on observed outcomes

In agreement with our hypothesis, we found that introduced dung beetle species had a similar influence on nutrient cycling as native species, suggesting that dung beetle introductions are beneficial to ecosystem functioning (Figure 2.9). However, nutrient cycling is a complex process that involves multiple factors, such as the physical and chemical properties of the soil, the presence of other organisms, and environmental conditions like temperature and moisture (Swift et al., 1998). As a result, the impact of introduced species on nutrient cycling may be influenced by these other factors, which could mask or amplify any differences in effects between introduced and native species. The outcome of the subgroup analysis of introduced versus native dung beetles for the remaining ecosystem functions should be interpreted with some caution due to the low sample size for introduced species.

We found a significant positive effect of dung removal by native dung beetle assemblages, suggesting that dung beetles in their natural distributional ranges are better adapted to those environments and may be more functionally efficient as a result. This has been demonstrated in other insects and arthropods, which benefit from access to native vegetation cover in agricultural habitats, providing enhanced ecosystem services, such as pollination (Isaacs et al., 2009). However, habitats where introduced dung beetles are found are subject to ongoing anthropogenic disturbances, such as tillage, pesticide application, and livestock trampling, which may affect the level of ecosystem functions. There has been recent debate about possible unintended consequences of introductions of non-native species (Pokhrel et al., 2020), however this is not based on quantitative evidence to date. While we found a significant negative effect of introduced dung beetles on plant growth enhancement, this is likely because of a small sample size (Figure 2.11). These outcomes highlight the need for further efforts to quantify and compare native versus introduced dung beetle effects on ecosystem functions.

No significant difference was found between lab and field studies for dung removal, nutrient cycling, plant growth enhancement, and secondary seed dispersal, indicating reliable results of dung beetle mediated ecosystem functioning. However, we did observe a greater effect of bioturbation in field studies compared to laboratory experiments (Figure 2.10). This difference could be attributed to variations in the methods used to measure bioturbation which include visual scoring (Leiva & Sobrino-Mengual, 2023), collection of upturned soil from the surface (Ferreira et al., 2023) and bulk density (Maldonado et al., 2019; Manning, Slade, et al., 2017). Furthermore, the volume and substrates used in laboratory experiments may be less compacted, requiring less effort for bioturbation to occur (Reis et al., 2023).

Dung removal was greatest in observational studies, which is likely because the dung was exposed to an uncontrolled diversity and abundance of dung beetles over time, compared to experimental studies which have highly controlled dung beetle biomass, abundance, or diversity. This is similar to the effect we found with mixed nesting behaviour, highlighting the potentially critical role of complementarity effects in driving rates of ecosystem functioning. Another explanation could be due to the methods used to quantify dung removal which could lead to differences in the observed outcomes. For example, observational studies may use different sampling methods or may not be able to account for the fate of dung that is removed by other organisms in addition to dung beetles. We observed no difference in bioturbation or secondary seed dispersal in observational versus experimental studies. This suggests that these ecological processes may be more consistent and independent of the study method, highlighting the robustness of the observed outcomes. Finally, we found nutrient cycling was greater in experimental studies, however this result is not particularly reliable because of the low sample size from published studies (Figure 2.9).

Data limitations and conclusions

Despite intensive efforts to conduct a comprehensive search for primary publications with relevant data, some papers may have been missed due to the limitations of the search terms. While the naïve search generated a large number of studies, the use of natural language processing methods revealed that the terminology used in this field can be rather broad. As a result, not all authors will include terms like “dung beetle” and “ecosystem function” in their abstract or title, and instead may use completely different and more descriptive terminology. Manually searched studies were not included here, which is a limitation to the outcomes of our study. To capture all published research on dung beetle-mediated ecosystem processes, additional manual searches for studies may have been beneficial for identifying research that does not use the common terminology found in the dung beetle ecology literature, but that may be reported in other disciplines such as environmental engineering (Grames et al., 2019).

Studies investigating dung beetle impacts on ecosystem functions often focused heavily on community factors such as dung beetle abundance, richness, and identity. While these attributes are important, they were often discussed in detail without explicit examination of the subsequent ecological processes resulting from dung beetle activity. As a result, 249 papers were excluded from the meta-analysis. This could be mitigated by developing and using a standardized protocol for dung beetle ecology research, which would yield valuable insights into the relationships between dung beetle community factors, as well as provide a more comprehensive understanding of the effects of dung beetles on ecosystem functions and services. Furthermore, adopting a standardized reporting system could assist future quantitative synthesis exercises, such as meta-analyses, by improving reporting transparency and preventing the damaging “file drawer problem” (Koricheva et al., 2013). This would enhance comparative power between different factors, such as ecosystem type.

The meta-analysis method constrained us to consider only studies that report both control (absence of dung beetles) and treatment (presence of dung beetles) outcomes (Osenberg et al., 1999). As a result, the final dataset included studies that reported the outcomes of control treatments, which are necessary for calculating effect sizes. Consequently, we had to eliminate 63 studies which would have contributed 297 effect sizes to our analyses. Most of the studies that were removed were from tropical settings and wild environments, and despite authors mentioning the use of dung-only controls, they did not report this data in a graph or table form in the paper. Obtaining these data by contacting the authors of these studies would be advantageous for future research, especially since they represent the geographical gaps in our analysis, for example from Southeast Asian tropical rainforests, which have a significant amount of literature on dung beetles but were unfortunately excluded due to lack of reporting on control treatments.

Our meta-analysis specifically focuses on the responses of multiple ecosystem functions to the presence or absence of dung beetles. While there are benefits in concentrating on the functions derived from dung beetle presence in particular, we acknowledge some disadvantages to this, in that it removes potentially fundamental mechanisms for evaluating dung beetle mediated ecosystem functioning, such as abundance and richness effects on ecosystem functioning (Barragán et al., 2011, 2021; Manning & Cutler, 2018b; Sarmiento-Garcés & Hernández, 2021). To address this gap, future research could consider data-mining community attributes and using meta-regression methods to assess the effects of abundance and richness on separate ecosystem functions. In addition to this, there may be an impact of varying dung availability on dung beetle resource use rates. A potential future research direction could also investigate the quantity of dung used in experimental treatments. If an excessive amount is used, it may mask the effects of competition among dung beetles and have repercussions for predicted ecosystem functions (Carvalho et al., 2018).

In summary, our findings indicate that dung beetles exert significant effects on various ecosystem functions, such as trophic regulation, nutrient cycling, plant growth enhancement, dung removal, bioturbation, and secondary seed dispersal. The extent to which these functions are enhanced, however, is contingent on factors such as nesting behaviour, ecosystem type, and variation in study methodologies. Since the impacts of dung beetles are highly context-dependent, repeated observations and experiments conducted across multiple geographic locations, ecosystem types and across gradients of anthropogenic disturbance are necessary to enhance our understanding of the mechanisms underlying their effects. Given the rapid pace of environmental change, it is crucial to determine the overall effects of dung beetle-mediated ecosystem processes. Doing so will enable predictions of the functional consequences of changing dung beetle biodiversity, as well as development of targeted strategies for managing ecosystems and the functions and services they provide.

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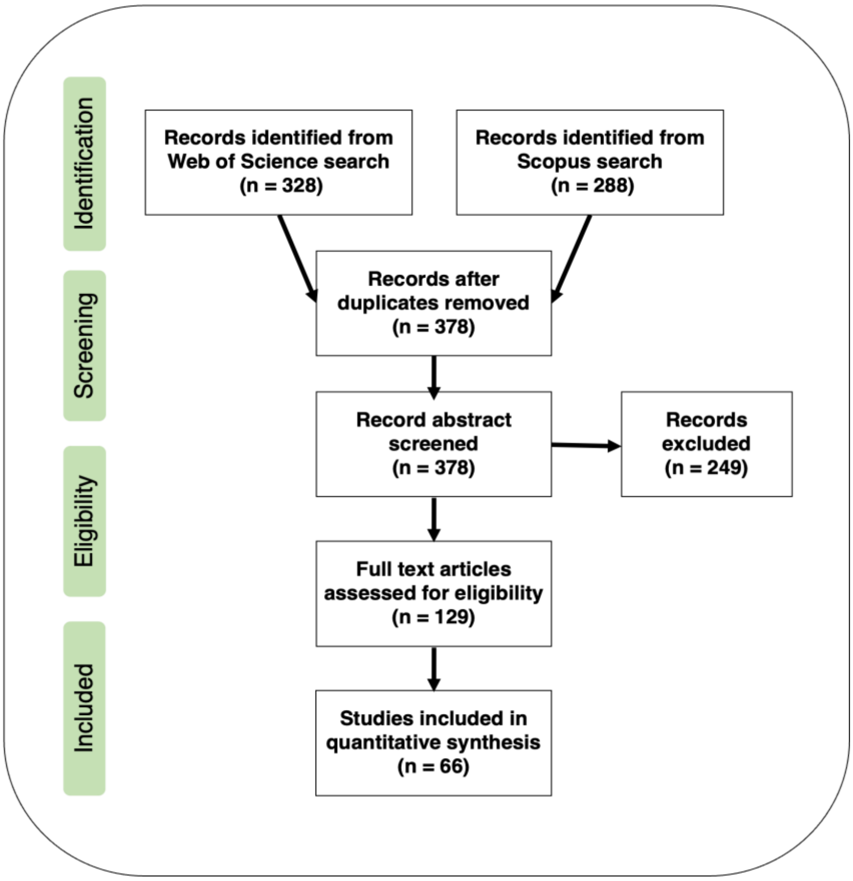
Appendices

Appendix 0.1 Prisma flow diagram showing the systematic selection of primary literature.

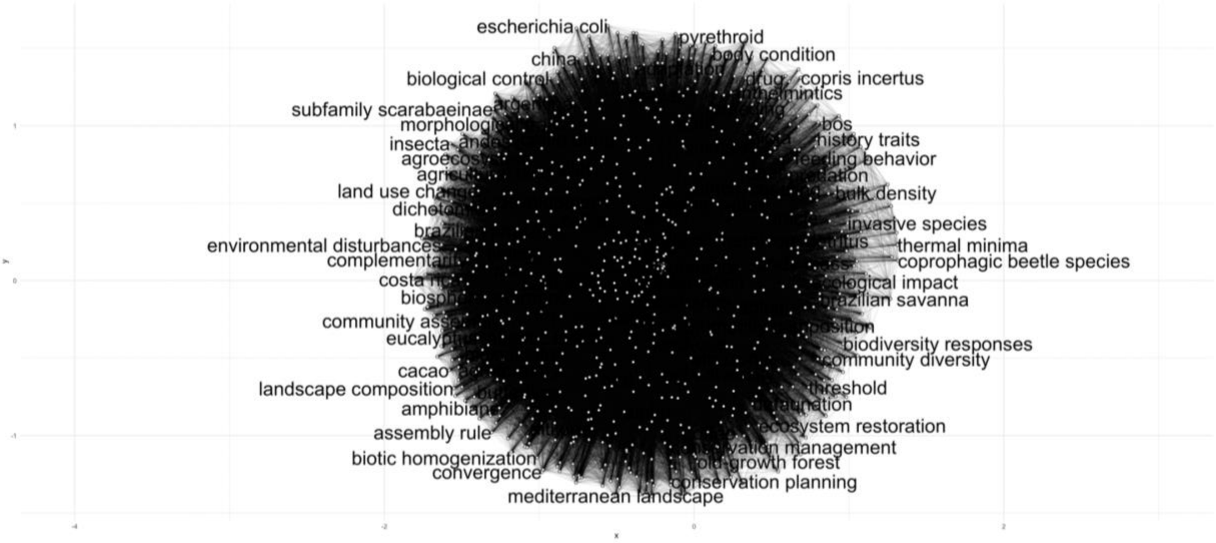


Appendix 0.2 Dung beetle stop words

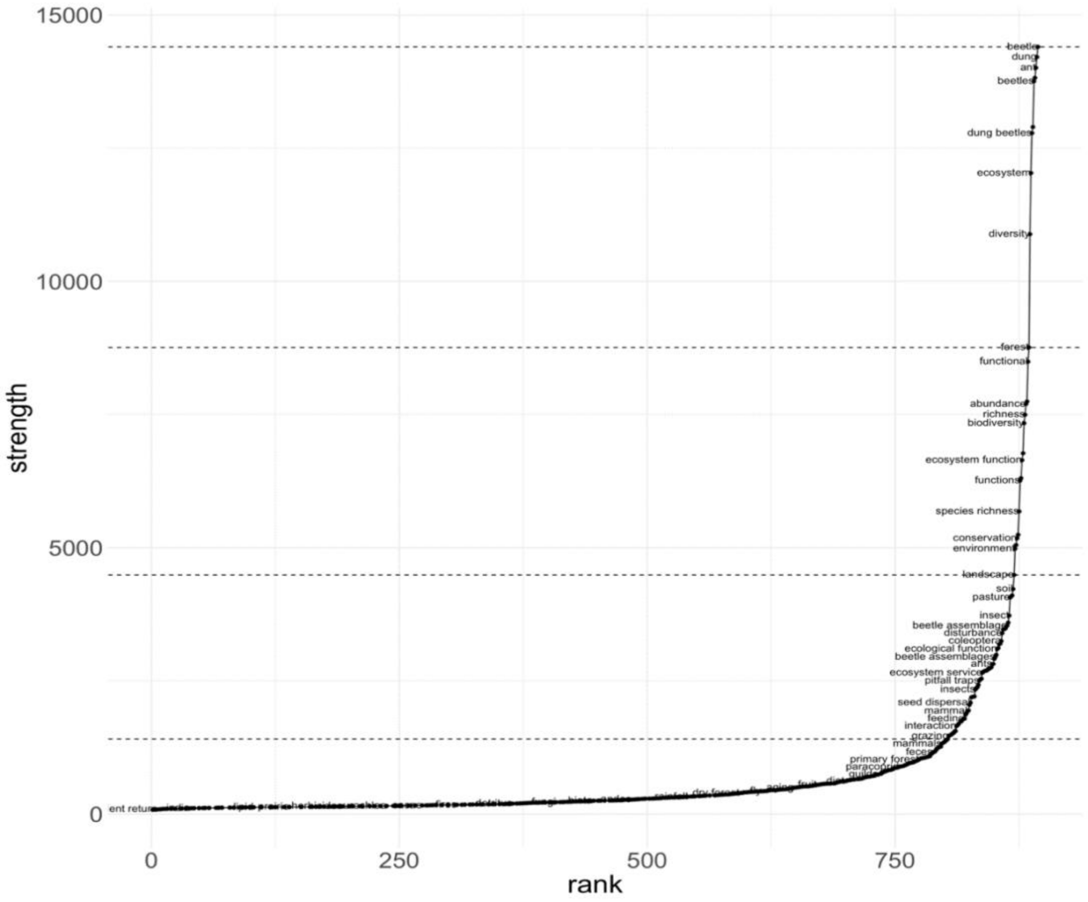
Dung beetle ecology stop words

access
adverse
affected
aimed
amounts
analyses
analysis
appeared
areas
article
aspects
association
attribution
author
balanced
based
belonging
berlin
biotropica
blackwell
british
business
cambridge
causing
challenge
collected
commons
compared
contributed
correlated
correlation
correspondence
creative
critically
current
degrees
delivery
demonstrate
demonstrated
demonstrates
differ
differed
differences
differently
direct
distributed
effect
effects
effort
elsevier
empirical
essential
evaluated
evidence
examined
excellent
exclusive
expansion
explanatory
factors
fewer
findings
focused
found
future
global
greater
group
groups
heidelberg
higher
highlight
identified
impact
implications
important
including
increased
individuals
influence
influenced
information
international
involved
knowledge
large
levels
licence
license
limited
lower
maintaining
major
manipulative
masson
material
media
medical
methods
model
multiple
nacional
needed
negative
number
online
original
oxford
perform
periodicals
periods
permits
points
poorly
positive
positively
potential
predictor
present
press
previous
producing
products
protocols
provide
providers
providing
published
publishing
rapid
reduced
regime
region
related
relationship
remain
remains
represent
research
reserved
respond
results
revealed
rights
royal
sampling
science
sensu
service
shifts
showed
showing
shows
significant
significantly
sites
small
sociedade
society
springer
springer-verlag
standardized
stricto
strong
studied
studies
study
suggest
suggests
support
times
understood
unequally
universidad
university
unknown
unrestricted
urgently
valuable
values
variables
variation
varied
varying
widely
wiley

Appendix 0.3 Key terms co-occurrence network identifying words that are central to the field of study. Terms in the center of the network are of greater importance than those found on the edges.



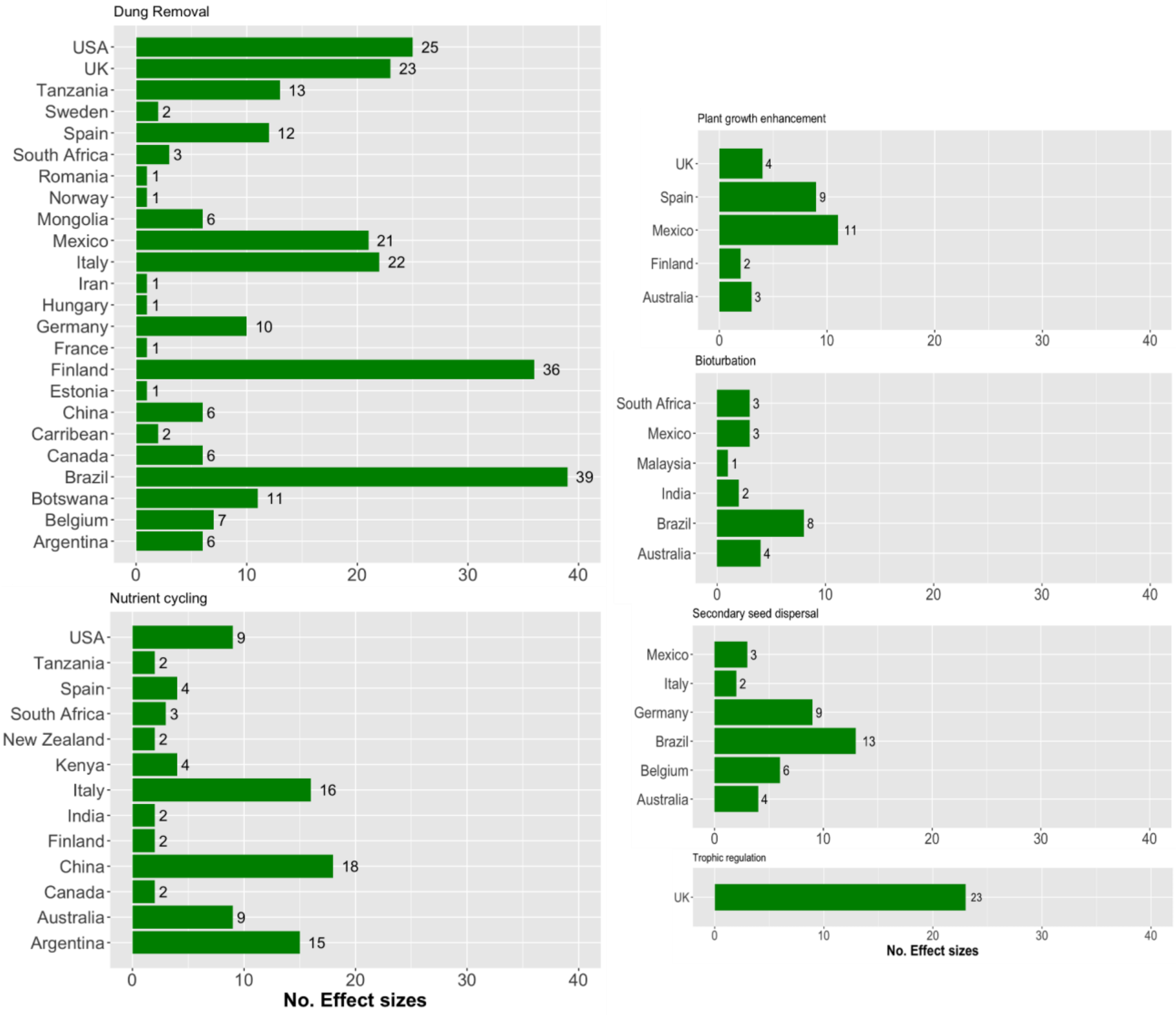
Appendix 0.4 Ranked node strengths of the terms found in the co-occurrence network with cumulative cut off points which returns the minimum number of terms that will give the percent strength of the network. Node strength is a weighted measure of how important a measure is in the network and terms with greater node strengths have more occurrences.



Appendix 0.5 Concept groups following the PICO framework for filtering search terms to produce the final search. Groups were codified as follows: 1 = beetles, 2 = dung, 3 = ecological outcomes, 4 = processes.

Group	Description
1	***Synonyms for dung beetle*** Dung beetle, Scarabaeinae
2	***Synonyms for dung*** Dung, manure
3	***Ecological outcomes relating to dung beetles*** Ecosystem function, ecosystem process, ecosystem service
4	***Potential processes as a result*** Decomposition, bioturbation, nutrient cycling, flux, recycling, primary production, biomass production, plant growth, secondary seed dispersal, pollination

Appendix 0.6 Bar charts showing the number of effect sizes extracted from studies from each country



Appendix 0.7 Results of meta analyses on study-level factors of **overall effect**. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes Hedges' g, the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom (df)and the p-value.

	Effect size				**Test statistics**				
Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
Dung Removal ($Q_{\text{difference}}$)	68.79	[26.08, 111.51]	21.79	0.0016	1719.15	25.80	91.76%	3	< .0001
No Moderators (Q_{overall})	109.14	[85.31, 132.97]	12.16	<.0001	37240.32	13100.05	100.00%	255	< .0001
Paracoprid	67.56	[38.59, 96.51]	14.78	<.0001	9084.99	1902.08	99.99%	44	< .0001
Endocoprid	39.73	[21.93, 57.52]	9.08	<.0001	2021.59	1283.24	99.96%	26	< .0001
Telecoprid	39.61	[18.16, 61.05]	10.94	0.0003	2055.46	636.28	99.88%	18	< .0001
Mixed	135.30	[100.34, 170.25]	17.83	<.0001	52714.43	8885.82	100.00%	167	< .0001
Nutrient Cycling ($Q_{\text{difference}}$)	223.45	[46.15, 400.74]	90.46	0.014	24649.49	26.21	84.30%	3	< .0001
No Moderators (Q_{overall})	301.68	[197.71, 405.64]	53.04	<.0001	487.19	5555.86	100.00%	87	< .0001
Paracoprid	294.81	[142.52, 447.09]	77.70	0.001	204044.46	2226.88	100.00%	34	< .0001
Endocoprid	440.33	[97.07, 783.58]	175.13	0.012	454707.93	1494.75	100.00%	14	< .0001
Telecoprid	23.60	[7.59, 39.60]	8.17	0.0039	503.90	225.54	99.70%	8	< .0001
Mixed	282.64	[112.68, 452.60]	86.72	0.0011	206082.75	1315.21	100.00%	28	< .0001
Bioturbation ($Q_{\text{difference}}$)	202.71	[-153.02, 558.43]	181.50	0.260	98.58	70.20	98.60%	1	< .0001
No Moderators (Q_{overall})	81.18	[24.00, 138.34]	29.17	0.010	14578.49	471.44	100.00%	20	< .0001
Paracoprid	23.76	[18.65, 28.86]	2.61	<.0001	12.45	5.30	61.30%	2	0.0707
Telecoprid	386.79	[302.02, 471.55]	43.25	<.0001	0.00	0.01	0.00%	1	0.9043

Plant Growth Enhancement ($Q_{difference}$)	123.65	[58.47, 188.83]	33.26	0.000	2662.54	7.70	62.40%	3	0.0527
No Moderators ($Q_{overall}$)	175.41	[102.92, 247.89]	36.98	<.0001	38354.58	1000.05	100.00%	28	< .0001
Paracoprid	62.74	[6.41, 119.05]	28.73	0.029	5527.95	178.30	99.96%	6	< .0001
Endocoprid	119.57	[52.76, 186.37]	34.09	0.0005	3018.51	11.70	89.68%	2	0.0029
Telecoprid	121.31	[24.26, 218.36]	49.52	0.0143	4426.63	9.83	89.83%	1	0.0017
Mixed	241.96	[124.89, 359.03]	59.73	<.0001	58612.49	641.96	100.00%	16	< .0001
Secondary Seed Dispersal ($Q_{difference}$)	96.43	[27.50, 165.35]	35.17	0.010	1677.95	2.65	62.20%	1	0.1036
No Moderators ($Q_{overall}$)	74.13	[44.44, 103.81]	15.15	<.0001	8010.87	914.34	99.80%	35	< .0001
Paracoprid	143.68	[60.72, 226.64]	42.33	0.0007	2563.17	3.30	69.71%	1	0.0692
Mixed	70.26	[39.64, 100.86]	15.62	<.0001	8087.98	878.96	99.85%	33	< .0001
Trophic Regulation ($Q_{difference}$)	330.80	[250.57, 411.01]	40.93	<.0001	0.00	1.93	0.00%	2	0.3813
No Moderators ($Q_{overall}$)	341.72	[239.08, 444.35]	52.37	<.0001	60862.33	631.48	99.70%	23	< .0001
Paracoprid	668.39	[183.83, 1152.94]	247.23	0.0069	106370.91	7.33	86.36%	1	0.0068
Endocoprid	323.32	[233.60, 413.04]	45.78	0.0015	101969.38	272.34	99.99%	10	< .0001
Mixed	311.86	[119.09, 504.63]	98.35	0.0015	101969.38	272.34	99.99%	10	< .0001

Appendix 0.8 Results of meta analyses of **dung removal** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (Hedges’ g), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (**τ^2**), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No Moderators	**($Q_{overall}$)**	**109.145**	**[85.31, 132.97]**	**12.160**	**< .0001**	**37240.320**	**13100.047**	**100.00%**	**255**	**< .0001**
Latitude	Tropical	52.367	[40.22, 64.50]	6.193	< .0001	3299.687	3175.553	99.96%	92	< .0001
	Temperate	139.007	[101.82, 176.19]	18.971	< .0001	57894.323	9914.827	100.00%	162	< .0001
	($Q_{difference}$)	93.832	[9.00, 178.65]	43.280	0.0302	3554.112	18.848	94.96%	1	< .0001
Landscape	Production	134.964	[99.32, 170.60]	18.183	< .0001	55509.149	9669.169	100.00%	169	< .0001
	Wild	48.365	[39.45, 57.29]	4.552	< .0001	1602.290	3395.338	99.92%	85	< .0001
	($Q_{difference}$)	89.875	[5.08, 174.66]	43.263	0.0378	3574.017	21.345	95.31%	1	< .0001
Habitat	Agriculture	70.467	[57.17, 83.75]	6.779	< .0001	6924.925	6764.641	99.98%	157	< .0001
	Desert	99.195	[33.37, 165.01]	33.585	0.0031	2118.657	16.096	93.79%	1	< .0001
	Forest	36.784	[28.74, 44.82]	4.103	< .0001	826.919	1880.493	99.86%	53	< .0001
	Grassland	336.132	[211.10, 461.16]	63.793	< .0001	168803.726	4020.353	99.99%	41	< .0001
	($Q_{difference}$)	124.018	[4.75, 243.27]	60.848	0.0415	13660.599	41.137	99.35%	3	< .0001
Introduced / Native	Introduced	52.228	[14.75, 89.70]	19.119	0.0063	1958.134	38.692	98.18%	5	< .0001
	Native	110.527	[86.08, 134.96]	12.470	< .0001	38251.491	12962.311	100.00%	249	< .0001
	($Q_{difference}$)	83.179	[26.15, 140.20]	29.094	0.0042	1438.866	6.523	84.67%	1	0.0106
Study Type	Laboratory	102.377	[63.53, 141.21]	19.816	< .0001	15214.542	1327.201	99.99%	40	< .0001
	Field	109.187	[81.89, 136.47]	13.925	< .0001	41152.816	11764.509	100.00%	214	< .0001
	($Q_{difference}$)	106.936	[84.60, 129.26]	11.393	< .0001	0.000	0.000	0.00%	1	0.7786

Observational / Experimental	Observational	174.130	[120.16, 228.09]	27.534	< .0001	78844.075	6730.774	100.00%	104	< .0001
	Experimental	52.052	[120.16, 228.09]	5.023	< .0001	3537.200	6369.143	99.96%	150	< .0001
	($Q_{\text{difference}}$)	110.089	[120.16, 228.09]	60.965	0.071	7059.773	19.025	94.74%	1	< .0001

Appendix 0.9 Results of meta analyses of **nutrient cycling** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**(Q_{overall})**	301.6822	[197.71, 405.64]	53.0436	< .0001	237352.0825	5555.8576	100.00%	87	< .0001
Latitude	Tropical	18.5173	[9.16, 27.87]	4.773	0.0001	433.9885	476.6099	99.72%	22	< .0001
	Temperate	361.103	[232.43, 489.77]	65.6499	< .0001	273767.9584	4671.848	100.00%	64	< .0001
	($Q_{\text{difference}}$)	183.5531	[-151.95, 519.05]	171.1786	0.2836	56516.1622	27.0883	96.31%	1	< .0001
Landscape	Production	86.3159	[57.38, 115.24]	14.7585	< .0001	12433.5223	3305.534	99.98%	61	< .0001
	Wild	817.7227	[493.74, 1141.69]	165.2959	< .0001	663047.1007	2148.8083	99.99%	25	< .0001
	($Q_{\text{difference}}$)	433.49	[-282.35, 1149.33]	365.2337	0.2353	253707.6779	19.4243	94.85%	1	< .0001
Habitat	Agriculture	90.7476	[59.05, 122.44]	16.1709	< .0001	14212.8496	2955.1305	99.98%	58	< .0001
	Forest	30.0763	[9.49, 50.66]	10.5033	0.0042	756.313	348.508	98.47%	8	< .0001
	Grassland	900.0261	[548.51, 1251.53]	179.3443	< .0001	616573.2022	1171.1642	99.93%	19	< .0001
	($Q_{\text{difference}}$)	313.6796	[-208.16, 835.52]	266.2516	0.2387	202837.2708	32.4116	99.80%	1	< .0001
Introduced / Native	Introduced	293.5306	[104.54, 482.51]	96.4234	0.0023	137226.7262	540.8728	100.00%	15	< .0001
	Native	300.934	[104.54, 482.51]	61.152	< .0001	259194.9418	5013.0458	100.00%	71	< .0001
	($Q_{\text{difference}}$)	298.8104	[197.59, 400.02]	51.6421	< .0001	0	0.0042	0.00%	1	0.9483

Study Type	Laboratory	291.2607	[2.68, 579.83]	147.2357	0.0479	82954.2486	65.3948	99.78%	3	< .0001
	Field	303.5581	[194.52, 412.59]	55.6322	< .0001	249168.8102	5411.2495	100.00%	83	< .0001
	($Q_{\text{difference}}$)	302.0218	[200.02, 404.02]	52.0412	< .0001	0	0.0061	0.00%	1	0.9377
Observational / Experimental	Observational	28.8178	[6.49, 51.14]	11.39	0.0114	235.2589	10.2999	90.29%	1	0.0013
	Experimental	309.1748	[202.64, 415.70]	54.3507	< .0001	243423.7759	5502.529	100.00%	85	< .0001
	($Q_{\text{difference}}$)	163.9594	[-110.60, 438.52]	140.0879	0.2418	37758.1395	25.4886	96.08%	1	< .0001

Appendix 0.10 Results of meta analyses of **bioturbation** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**($Q_{overall}$)**	81.178	[24.01, 138.34]	29.169	0.005	14578.487	471.442	100.00%	20	< .0001
Latitude	Tropical	69.125	[14.59, 123.65]	27.820	0.013	13163.144	417.446	100.00%	17	< .0001
	Temperate	3997.373	[2929.26, 5065.48]	544.963	< .0001	0.000	0.196	0.00%	2	0.9067
	($Q_{difference}$)	1995.546	[-1853.35, 5844.44]	1963.762	0.310	7566688.285	51.824	98.07%	1	< .0001
Landscape	Production	905.549	[-9.03, 1820.14]	466.634	0.052	2204993.042	126.767	100.00%	10	< .0001
	Wild	75.014	[-13.86, 163.89]	45.349	0.098	19912.202	337.857	100.00%	9	< .0001
	($Q_{difference}$)	360.431	[-412.66, 1133.52]	394.444	0.361	234992.025	3.138	68.13%	1	0.0765
Habitat	Agriculture	905.549	[-9.03, 1820.13]	466.634	0.052	2204993.042	126.767	100.00%	10	< .0001
	Forest	102.169	[-30.57, 234.90]	67.726	0.131	31122.183	124.639	100.00%	6	< .0001
	Grassland	23.758	[18.65, 28.86]	2.606	< .0001	12.452	5.298	61.30%	2	0.0707
	($Q_{difference}$)	46.378	[-26.54, 119.30]	37.209	0.213	1777.008	4.908	28.32%	2	0.0859
Study Type	Laboratory	23.758	[18.65, 28.86]	2.606	< .0001	12.452	5.298	6130.00%	2	0.0707
	Field	100.076	[28.04, 172.11]	36.751	0.007	19374.174	254.201	100.00%	17	< .0001
	($Q_{difference}$)	53.113	[-19.65, 125.88]	37.129	0.153	2233.474	4.291	76.96%	1	0.0383
Observational / Experimental	Observational	163.389	[50.19, 276.58]	57.752	0.005	24742.009	124.596	100.00%	7	< .0001
	Experimental	665.837	[-73.66, 1405.33]	377.303	0.078	1703056.204	326.396	100.00%	12	< .0001

($Q_{\text{difference}}$)	276.268	[-134.73, 687.27]	209.700	0.188	53380.664	1.733	42.29%	1	0.1881

Appendix 0.11 Results of meta analyses of **plant growth enhancement** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**($Q_{overall}$)**	175.411	[102.92, 247.89]	36.984	<.0001	38354.582	1000.046	100.00%	28	<.0001
Latitude	Tropical	156.053	[0.71, 311.38]	79.255	0.049	67709.521	337.986	100.00%	10	<.0001
	Temperate	187.737	[112.66, 262.81]	38.304	<.0001	25138.928	661.151	99.97%	17	<.0001
	($Q_{difference}$)	181.737	[114.14, 249.33]	34.487	<.0001	0.000	0.130	0.00%	1	0.7189
Landscape	Production	194.662	[71.90, 317.41]	62.631	0.0019	45476.239	340.304	100.00%	11	<.0001
	Wild	162.237	[71.79, 252.68]	46.147	0.0004	35087.793	659.660	100.00%	16	<.0001
	($Q_{difference}$)	173.647	[100.83, 246.46]	37.152	<.0001	0.000	0.174	0.00%	1	0.6768
Habitat	Agriculture	159.891	[90.12, 229.65]	35.593	<.0001	25522.408	663.485	99.99%	20	<.0001
	Forest	218.100	[12.56, 423.63]	104.869	0.0375	86043.931	336.104	100.00%	7	<.0001
	($Q_{difference}$)	165.904	[99.84, 231.96]	33.705	<.0001	0.000	0.276	0.00%	1	0.5992
Introduced / Native	Introduced	-5.291	[-15.98, 5.39]	5.454	0.332	85.155	33.828	99.04%	2	<.0001
	Native	197.253	[119.90, 274.59]	39.462	<.0001	39019.472	965.328	100.00%	25	<.0001
	($Q_{difference}$)	92.210	[-106.14, 290.56]	101.202	0.3622	19718.476	25.850	96.13%	1	<.0001
Study Type	Laboratory	153.935	[100.06, 207.80]	27.485	<.0001	7543.649	102.232	95.83%	10	<.0001
	Field	189.246	[73.34, 305.14]	59.134	0.0014	61286.226	580.402	100.00%	17	<.0001
	($Q_{difference}$)	160.208	[111.35, 209.05]	24.925	<.0001	0.000	0.293	0.00%	1	0.5882

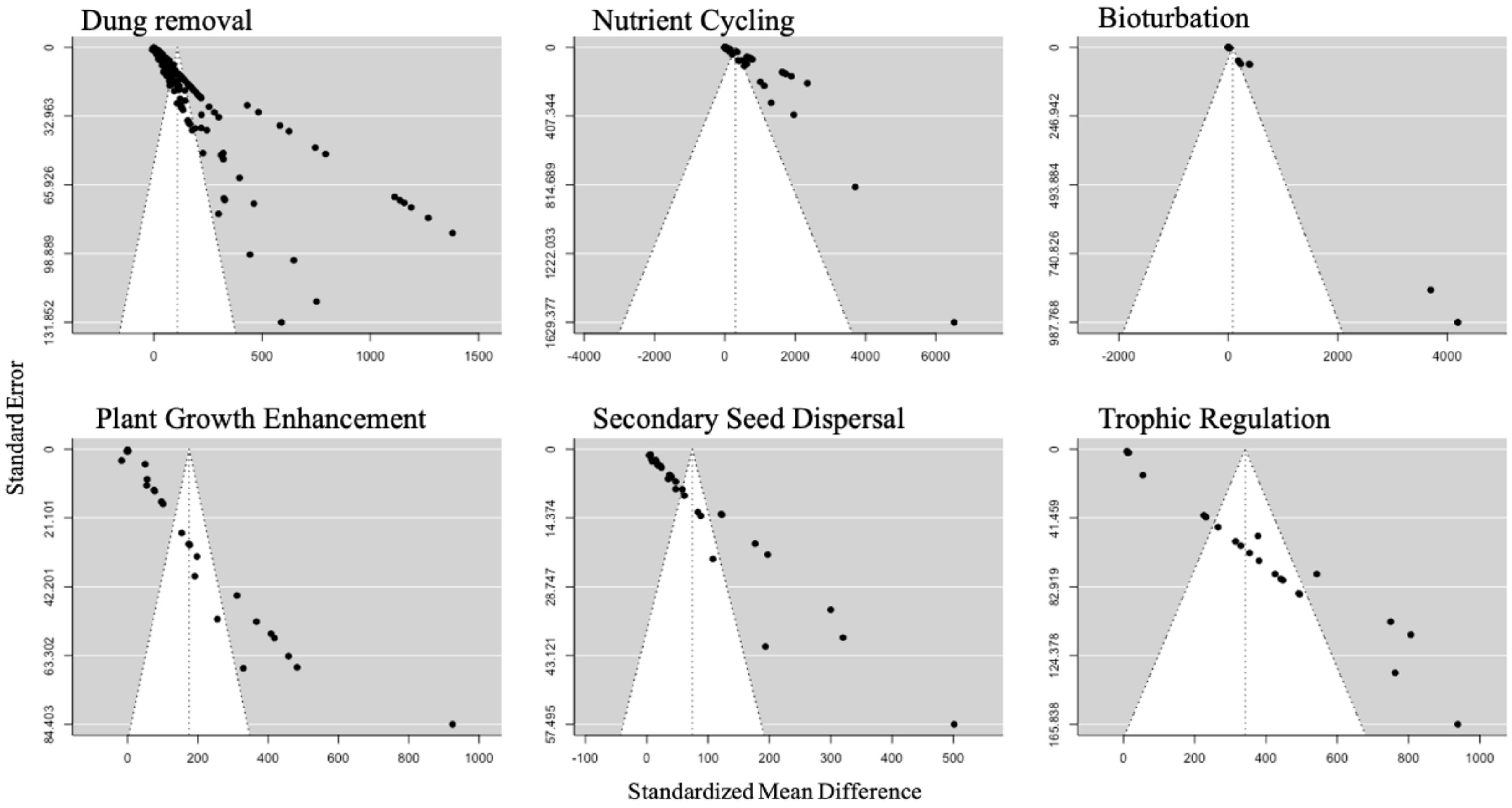
Appendix 0.12 Results of meta analyses of **secondary seed dispersal** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**($Q_{overall}$)**	74.128	[44.44, 103.81]	15.147	<.0001	8010.866	914.339	99.84%	35	<.0001
Latitude	Tropical	101.904	[48.81, 154.99]	27.085	0.0002	14317.615	664.536	99.90%	19	<.0001
	Temperate	34.952	[25.24, 44.65]	4.950	<.0001	329.619	247.120	95.50%	15	<.0001
	($Q_{difference}$)	63.133	[-1.65, 127.91]	33.055	0.0561	1862.274	5.913	83.09%	1	0.015
Landscape	Production	115.499	[41.17, 189.82]	37.923	< .0001	19571.126	437.455	99.91%	13	<.0001
	Wild	51.833	[30.52, 73.13]	10.871	<.0001	2515.848	460.793	99.48%	21	<.0001
	($Q_{difference}$)	73.299	[14.30, 132.28]	30.097	0.0149	1248.477	2.604	61.60%	1	0.1066
Habitat	Agriculture	115.499	[41.17, 189.82]	37.923	0.0023	19571.126	437.455	99.91%	13	<.0001
	Forest	52.560	[30.13, 74.98]	11.440	<.0001	2661.702	445.284	99.52%	20	<.0001
	Grassland	39.408	[27.73, 51.08]	5.956	<.0001	0.000	0.000	0.00%	0	1.000
	($Q_{difference}$)	47.912	[30.47, 65.34]	8.896	<.0001	96.367	4.703	38.80%	2	0.0952
Study Type	Laboratory	143.685	[60.72, 226.64]	42.329	0.0007	2563.169	3.301	69.71%	1	0.0692
	Field	70.258	[39.64, 100.86]	15.618	<.0001	8087.984	878.957	99.85%	33	<.0001
	($Q_{difference}$)	96.431	[27.50, 165.35]	35.168	0.0061	1677.947	2.649	62.24%	1	0.1036
Observational / Experimental	Observational	94.418	[11.59, 177.24]	42.259	0.0255	22782.854	313.209	99.96%	12	<.0001
	Experimental	64.920	[43.48, 86.35]	10.938	<.0001	2595.001	572.875	99.71%	22	<.0001
	($Q_{difference}$)	66.772	[46.01, 87.52]	10.589	<.0001	0.000	0.457	0.00%	1	0.4992

Appendix 0.13 Results of meta analyses of **trophic regulation** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

	Effect size				**Test statistics**				
Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators ($Q_{overall}$)	354.971	[250.65, 459.28]	53.223	<.0001	59990.167	624.373	99.97%	22	<.0001

Appendix 0.14 A funnel plot of the estimates (Standardized Mean Difference = Hedges' g) for the overall effects (no moderators) of each ecosystem function. Both the rank correlation and the regression test indicated potential funnel plot asymmetry at $p < 0.0001$ and $p < 0.0001$ for (a) dung removal; (b) nutrient cycling; (c) bioturbation; (d) plant growth enhancement; (e)secondary seed dispersal; and (f) trophic regulation.



Appendix 0.15 Data sources (alphabetical-order) list of 66 studies

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