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Contribution of Dung Beetles to the Enrichment of Soil with Organic Matter and Nutrients under Controlled Conditions

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Abstract: Dung beetles are important ecosystem engineers as they bury manure produced by animals and contribute to nutrient cycling. This study assessed the impact of four dung beetle species, a roller (*Gymnopleurus sturmi*) and three tunnelers (*Onthophagus vacca*, *Onthophagus marginalis* subsp. *andalusicus* and *Euonthophagus crocatus*), on manure removal and soil fertility by using microcosms in a greenhouse setting. The four species contributed significantly to the removal of manure from the soil surface and increased the nutrient content of the soil, notably potassium, phosphorus, and nitrogen, but the amount varied depending on the species. These results highlight the importance of dung beetles in facilitating soil organic matter and nutrient flows and the need to preserve their populations to support the sustainability of grazing systems.

Keywords: dung beetles; soil fertility; nutrients; dung decomposition; biodiversity conservation

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1. Introduction

The rapid growth of the human population and the increasing demand for food are applying unprecedented pressure on agricultural production, making soil health crucial [1]. However, soil degradation threatens the ability to support food production, thereby compromising global food security [2]. In many rural areas, livestock farming is the primary economic activity, often at the expense of ecosystem health. Therefore, understanding the complex relationships between land use, the land itself, local biodiversity, and the ecosystem services they provide is essential for sustainable land management.

Dung beetles (Coleoptera: Scarabaeidae) play a vital role in grazed ecosystems by significantly contributing to soil fertility [3–8]. These beetles feed on the microorganism-rich liquid in dung and use the fibrous material to raise their larvae [9]. By burying a substantial portion of the dung at various depths, depending on the species, they stimulate the activity of microorganisms responsible for nitrogen mineralization and nitrification [10]. Thus, dung beetle activity improves nutrient mobilization, soil aeration, and, consequently, soil fertility [11]. In addition to their contributions to soil fertility, dung beetles play a crucial role in regulating harmful fly populations, some of which are hematophagous and can affect livestock productivity [7,12]. Reducing these fly populations results in significant economic benefits for farmers [13]. While performing these ecosystem services, dung beetles act as ecosystem engineers because they modify habitat conditions and nutrient availability for other species [14,15]. However, land conversion due to intensive agriculture has resulted in a worldwide decline in insect fauna, with dung beetles being particularly affected [16–20]. Different land management practices, grazing intensities, and pasture management methods affect dung beetle assemblages, although the underlying mechanisms often remain unclear [7]. Previous studies reported either positive effects of increased grazing intensity due to greater dung availability [21,22] or negative effects due to habitat deterioration [21,23] and the use of veterinary pharmaceuticals [20,24,25]. The ecosystem services provided by dung beetles are well known and valued [26], but it was important to quantify the impact on soil fertility of very common dung beetles in Morocco [27] and explore their role as ecosystem engineers.

In this study, we evaluated the efficiency of four dung beetle species belonging to two different guilds—a roller species, *Gymnopleurus sturmi* (MacLeay, 1821), and three tunneler species, *Onthophagus marginalis* subsp. *andalusicus* Waltl, 1835, *Onthophagus vacca* (Linnaeus, 1767), and *Euonthophagus crocatus* (Mulsant & Godart, 1870)—in burying dung and also their role in soil fertility by analyzing soil nitrogen, phosphorus, potassium, and organic matter content, at different depths.

These species are currently being introduced into Australia as part of the Dung Beetle Ecosystem Engineers (DBEE) national research project [28], which aims to fill in the gaps in the distribution of exotic dung beetles in southern Australia used to degrade the dung of cattle, which are exotic to Australia, by introducing new species active in spring and originating from regions with a Mediterranean bioclimate. The project also aims to quantify the ecosystem services and economic benefits provided by dung beetles and is expected to provide significant benefits to livestock producers by improving soil health in grazing systems, reducing the spread of diseases and insect pests, such as bush flies, increasing pasture health, and reducing nutrient run-off into waterways.

The choice of the four dung beetle species described above is particularly relevant because in Morocco, they are active in spring and are very abundant in the study area [27], and they have different ways of using animal dung. Three of the species dig galleries under the dung and bury the excrement in pedotrophic nests, while the other species form balls of dung from the dung pad, which are then rolled some distance away and buried [29].

We hypothesized that dung burial by these four species increases nutrient concentrations in the soil by incorporating surface dung into the soil and constructing galleries that facilitate the movement of nutrients through the soil profile. To test this hypothesis, we experimentally assessed organic matter and nutrient incorporation into the soil at three different depths by the four dung beetle species. Our aim was to understand the impact of dung beetles on the distribution of organic matter and nutrients in the soil by targeting the levels where dung beetle activity was most significant and where changes in nutrients were most likely to be observed, as determined in preliminary testing.

2. Materials and Methods

2.1. Background to This Study and Species Selection

The dung beetles *Onthophagus vacca*, *O. m. andalusicus*, *E. crocatus*, and *G. sturmi* were collected in April 2022 in the rural district of Ain Aicha in the province of Taounate, Morocco (34°28′59.99″ N–4°41′59.99″ W). These species were chosen because of their activity in spring, which makes them particularly relevant to this study. Quite similar in size, they differ in their behavior: the first three species belong to the guild of tunnelers, while *G. sturmi* is a roller species (Table 1). Rollers form balls of dung that they roll and bury some distance from the source, whereas tunnelers bury dung at or very near the source by burying it at varying depths, depending on the species.

Specimens were collected from cattle dung and the soil below and brought back to the laboratory. Beetles were installed in microcosms in a greenhouse with the temperature maintained to reflect natural conditions, thereby favoring the activity of all species. It is noteworthy that during a prior laboratory breeding experiment, all species were active and successfully produced brood balls from April to late May, except for *E. crocatus*. Although the full reproductive cycle of *E. crocatus* was not completely observed, egg-laying and brood ball production were documented. Overall, this species demonstrated substantial dung burial activity, highlighting its role in nutrient recycling and soil fertility enhancement.

Table 1. Life traits of the dung beetle species used in this study specifying their guild, body length (mm), and activity period.

Species	Dung Relocation Behavior	Body Length	Activity Period
Gymnopleurus sturmi	Roller	8–18	Spring-summer
Onthophagus vacca	Tunneler	7–13	Spring
Onthophagus marginalis subsp. *andalusicus*	Tunneler	6–12	Spring
Euonthophagus crocatus	Tunneler	6–12	Spring

2.2. Experimental Procedure

For the dung beetle microcosm experiment, we followed the protocol proposed by Barragán et al. [30]. The beetles were placed in containers, with three replicates for each species. Each container housed both sexes of each species (five males and five females), as they generally act as mating pairs. Additionally, we included two control groups, each with three replicates: "only dung controls" (dung deposited on the soil, without beetles) to account for dung dehydration and soil nutrient changes due to factors other than dung beetle activity and "only soil controls" (no manure nor dung beetles). This allowed us to assess the effect of beetles on nutrient recycling.

The size of containers, 10 cm in diameter and 25 cm in depth was selected after a preliminary study evaluating different sizes, with the beetles nesting no deeper than 18 cm. The containers were filled with soil collected from the original site, characterized by a loamy-clay texture, with mainly clay (38.8%), fine silt (35.1%), and sand (18%). Each container was supplied with 100 g of fresh cow dung. All the containers were covered with wire mesh to prevent the beetles' escape. Every three days over the following 40 days, 100 g of fresh dung was supplied, and the manure remains were weighed to quantify manure removal rates. To ensure measurement consistency, we weighed the dung residues while still wet, both in the containers with the beetles and in the controls. Despite the potential variability in the drying process, standardizing the weighing procedure at regular intervals and under similar conditions makes it possible to characterize the changes in dung weight attributed to beetle activity [30].

2.3. Soil Sample Collection and Chemical Analyses

After 40 days, 100 g samples of soil were collected from all the containers (beetles and controls) at three depths: 0–7 cm, 7–14 cm, and 14–21 cm. We first collected a blend of 100 g of soil from the 0–7 cm zone, and then the remaining topsoil from this layer was carefully removed before accessing the next zone (7–14 cm) to collect another 100 g sample of soil; then, the remaining soil in this soil layer was also removed to access the 14–21 cm zone to collect another 100 g sample. The samples were then air-dried, crushed, and analyzed to determine their nutrient (P, K, N) concentrations and organic matter content. Ammonium acetate was used to extract potassium from the soil; the Olsen method was employed to analyze phosphorus concentration, with phosphorus extracted using a 0.5 M $NaHCO_3$ solution adjusted to a pH of 8.5 [31,32]; moreover, the Kjeldahl method was utilized to measure nitrogen content [33,34] using Kjeldahl Catalyst (Cu-TiO_2) tablets [35]. To determine the organic matter (OM) content, the samples were heated to 500 degrees Celsius for 5 hours to completely evaporate the moisture and burn the OM and then weighed.

2.4. Data Analyses

The nutrient concentrations at different depths and dung removal proportions by different species were compared by using R software (version 4.1.3) [36]. An ANOVA and/or a Kruskal–Wallis test was performed for non-normal data, followed by post hoc comparisons using the anova, kruskal-wallis.test and HSD.test, and pairwise.wilcox.test functions of the stats and agricolae packages, respectively. R software and the stats and agricolae packages were used to compare nutrient concentrations at different soil depths and dung removal rates for the different species. When the conditions of normality and/or homoscedasticity were fulfilled, ANOVA was performed, followed by Tukey tests. Conversely, when these conditions were not satisfied, a Kruskal–Wallis test was used, followed by Wilcoxon tests. The statistical significance level was set at the 0.05 probability level.

3. Results

3.1. Nutrient Analyses

Nutrient concentrations varied with soil depth and dung beetle species. In this section, we compared soil potassium, phosphorus, and nitrogen concentrations for the four dung beetle species; the differences in organic matter levels were also analyzed for the three soil zones.

3.1.1. Potassium

Potassium concentrations varied significantly between the three soil zones for the four dung beetle species (Figure 1). Potassium concentration increased significantly ($p \leq 0.001$) compared with the "soil only" and "soil with dung" controls. In the first 1–7 cm, the highest concentration was recorded for *G. sturmi* (337.4 ± 26.5 mg/kg), followed by *O. vacca* (202.0 ± 38.4 mg/kg) and *E. crocatus* (180.5 ± 16.09 mg/kg), although the difference between the latter two species was not significant. The difference between *O. m. andalusicus* and the "only dung" control was not significant. Such differences between species were maintained at all depths. The differences in potassium concentration were not significant between the "only dung" and "only soil" controls, with the concentration in the "only soil" control being slightly lower than when dung was deposited alone on the surface (99.0 ± 0 mg/kg vs. 118 ± 2.56 mg/kg, respectively).

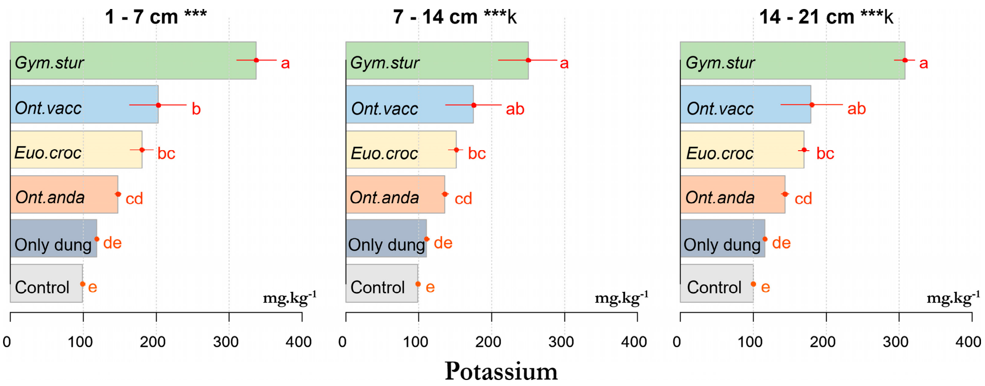

Figure 1. Potassium concentrations in the soil at different depth zones (1–7, 7–14, and 14–21 cm) resulting from dung beetle activity. *Gym. stur*: *Gymnopleurus sturmi*; *Ont. vacc*: *Onthophagus vacca*; *Euo. croc*: *Euonthophagus crocatus; Ont. anda*: *Onthophagus marginalis* subsp. *andalusicus*. Only dung = "Only dung control"; Control = "Only soil control" (no manure nor dung beetles). Means with the same letters are not significantly different. K: Kruskal-Wallis. *p*-values: *** ≤ 0.001.

3.1.2. Phosphorus

The phosphorus concentration increased significantly for the individual species and for the same species for depth (Figure 2) in comparison with the controls. For the 1–7 cm level, the highest phosphorus concentration was observed for *G. sturmi* (42.69 ± 4.09 mg/kg), which was significantly different ($p \leq 0.001$) from that of *E. crocatus* (35.60 ± 3.92 mg/kg), which was itself significantly different ($p \leq 0.001$) from those of both *O. vacca* (30.05 ± 2.93 mg/kg) and *O. m. andalusicus* (27.17 ± 1.96 mg/kg). For the 7–14 cm level, *E. crocatus* activity produced the highest phosphorus concentration (21.30 ± 0.42 mg/kg), followed by *O. andalusicus* (19.29 ± 1.35 mg/kg), but the difference between the two species was not significant. For the 14–21 cm level, phosphorus concentrations were highest for *O. m. andalusicus* and *O. vacca* (21.93 ± 0.38 mg/kg and 21.43 ± 1.23 mg/kg, respectively) but not significantly different from *E. crocatus* (19.74 ± 1.49 mg/kg), and the concentration for *G. sturmi* was slightly lower (18.7 ± 1.35 mg/kg). Overall, the phosphorus concentrations obtained for all species were significantly higher ($p \leq 0.001$) than those measured in the two controls ("only soil" and "only dung"; 8.68 ± 0 and 12.2 ± 2.35 mg/kg, respectively).

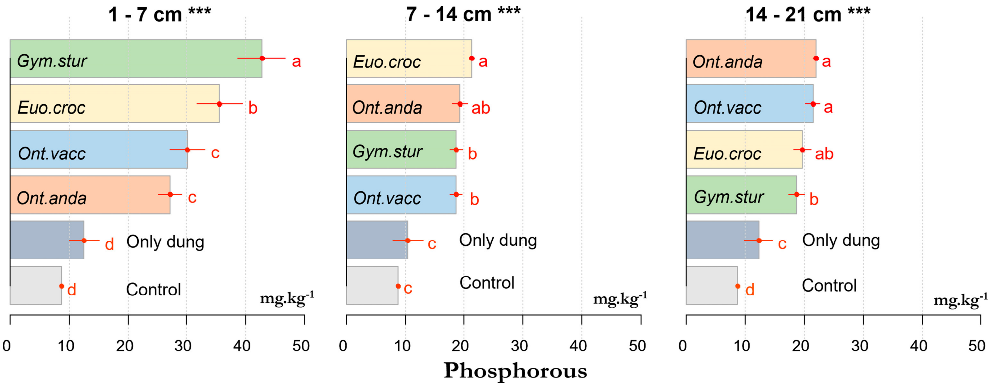

Figure 2. Phosphorus concentration in the soil at different depths (1–7, 7–14, and 14–21 cm) resulting from dung beetle activity. *Gym. stur*: *Gymnopleurus sturmi*; *Ont. vacc*: *Onthophagus vacca*; *Euo. croc*: *Euonthophagus crocatus*; *Ont. anda*: *Onthophagus marginalis* subsp. *andalusicus*. Only dung = "Only dung control"; Control = "Only soil control" (no manure nor dung beetles). Means with the same letters are not significantly different. K: Kruskal-Wallis. *p*-values: *** ≤ 0.001.

3.1.3. Nitrogen

The activity of the dung beetles resulted in much higher nitrogen concentrations in the soil than those initially found in the controls, whatever the soil depth (Figure 3). At all levels, *G. sturmi* contributed significantly more nitrogen to the soil ($p \leq 0.001$) (0.32 ± 0.06, 0.30 ± 0.05 and 0.30 ± 0.06 mg/kg for depths 0–7, 7–14 and 14–21 cm, respectively), compared with the "only soil" and "only dung" controls (0.03 ± 0 and 0.05± 0.01 mg/kg, respectively). *Euonthophagus crocatus* and *O. vacca* were significantly less efficient than *G. sturmi*, with nitrogen concentrations ranging from 0.12 ± 0.04 to 0.13 ± 0.06 mg/kg for *O. vacca*, depending on depth. *Onthophagus m. andalusicus* activity facilitated the lowest nitrogen level in the soil (0.10 ± 0.02 and 0.08 ± 0.01 mg/kg for depths 0–7 and 14–21 cm, respectively), although these values were still significantly higher than those of the controls.

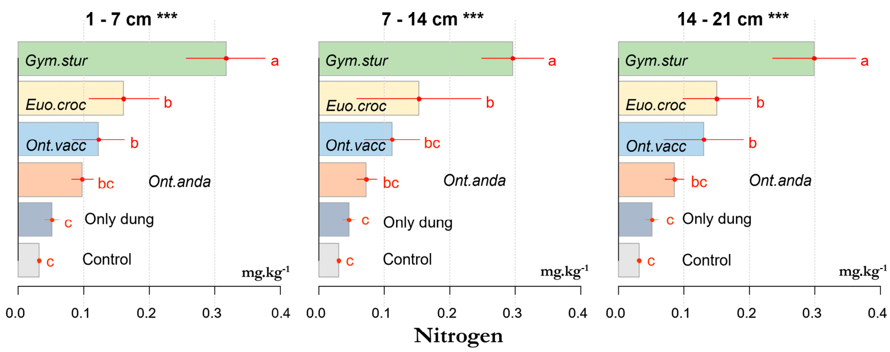

Figure 3. Nitrogen concentration in the soil at different depths (1–7 cm, 7–14 cm, and 14–21 cm) according to the dung beetle activity. *Gym. stur: Gymnopleurus sturmi*; *Ont.vacc: Onthophagus vacca*; *Euo. croc: Euonthophagus crocatus*; *Ont. anda: Onthophagus marginalis* subsp. *andalusicus*. Only dung = "Only dung control"; Control = "Only soil control" (no manure nor dung beetles). Means with the same letters are not significantly different. K: Kruskal-Wallis. *p*-values: *** ≤ 0.001.

3.1.4. Organic Matter

When the experiment was established, the initial organic matter content of the soil in the containers was 2.03 ± 0%. After 40 days, the activity of the dung beetles (dung buried for nesting) led to a significant increase in the organic matter content at all depths (Figure 4). *Gymnopleurus sturmi* regularly buried a significant amount of organic matter at all depths (6.24 ± 0.51, 5.53 ± 0.38 and 5.84 ± 0.39% at 0–7, 7–14, and 14–21 cm depth, respectively) ($p \leq 0.001$) but not in significantly higher amounts than *E. crocatus* (5.66 ± 0.49, 5.21 ± 0.38 and 5.66 ± 0.89% for the same depths, respectively. The quantity buried by *O. vacca* was significantly less ($p \leq 0.001$) than that buried by *G. sturmi* and *E. crocatus* at the three depth levels (5.11 ± 0.20, 4.41 ± 0.09 and 4.99 ± 0.34%, respectively), and *O. m. andalusicus* buried even less organic matter (4.57 ± 0.45, 3.73 ± 0.26 and 4.39 ± 0.51% at the three levels, respectively).

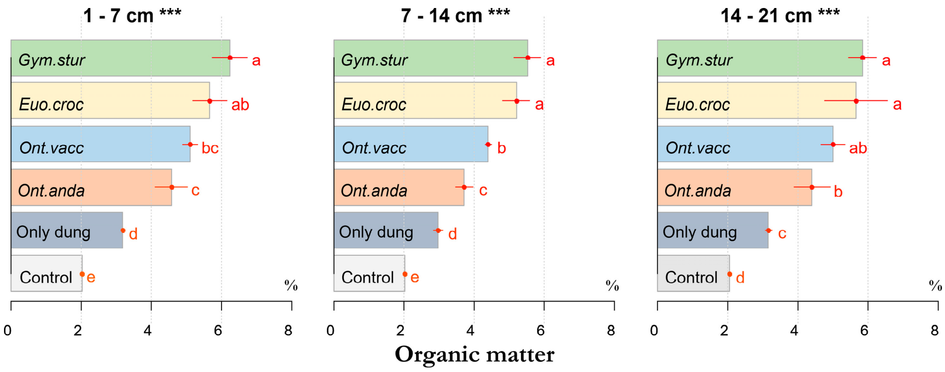

Figure 4. Organic matter content in the soil (%) at different depths (1–7 cm, 7–14 cm, and 14–21 cm) according to the dung beetle activity. *Gym. stur: Gymnopleurus sturmi*; *Ont.vacc: Onthophagus vacca*; *Euo.croc: Euonthophagus crocatus*; *Ont. anda: Onthophagus marginalis* subsp. *andalusicus*. Only dung = "Only dung control"; Control = "Only soil control" (no manure nor dung beetles). Means with the same letters are not significantly different. K: Kruskal-Wallis. p-values: *** ≤ 0.001.

3.2. Rate of Dung Removal by Dung Beetles

The ability of the different species to remove dung from the soil surface differed significantly ($p \leq 0.001$) (Figure 5). *Gymnopleurus sturmi* was the best-performing species, with a removal rate of 62.9 ± 0.50%, followed by *O. m. andalusicus* (58.33 ± 1.97%) and *O. vacca* (52.07 ± 1.07%), both differences being significant. *Euonthophagus crocatus* had a significantly lower removal rate (43.07 ± 1.50%; $p \leq 0.001$).

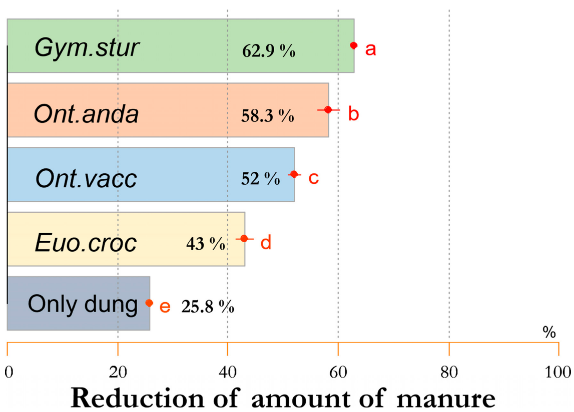

Figure 5. Comparison of reduction in amount of manure (%) when four dung beetles were present and in the control (only dung, without beetles). *Gym.stur: Gymnopleurus sturmi*; *Ont.vacc: Onthophagus vacca*; *Euo. croc: Euonthophagus crocatus*; *Ont. anda: Onthophagus marginalis* subsp. *andalusicus*. Means with the same letters are not significantly different; p-values ≤ 0.001.

In the absence of dung beetles (control "only dung"), the loss of dung weight at the surface (25.8 ± 0.35%) can be considered as the mean loss of water from the samples, which effectively reduced the percentage of wet dung removed by each of the different species. That moisture loss (25.8%) must be subtracted from the dung removal rate totals for each of the four species to obtain the effective removal rates, e.g., [62.9%–25.8%] for *G. sturmi.*

4. Discussion and Conclusions

In the present microcosm experiment, *G. sturmi*, *O. vacca*, *O. marginalis* subsp. *andalusicus*, and *E. crocatus* all contributed significantly to dung burial, leading to an enrichment of the different soil levels with organic matter and mineral nutrients, with different performance levels among the species. *Gymnopleurus sturmi* appeared to be more effective in enriching the soil with nutrients at all depths, achieved with a relatively high rate of removal of dung from the surface. Rollers handle dung differently from tunnelers, which may affect the distribution of nutrients. *Gymnopleurus sturmi* is larger than other species, allowing it to bury larger dung balls, explaining the higher nutrient levels and more efficient dung removal observed. It is interesting to note that although it was expected that the burrowing species, because of their ability to create complex galleries and accumulate large quantities of dung, would be more effective in enriching the deep layers of the soil, *G. sturmi* defied these expectations. This better performance could be attributed to the combination of its larger size and its unique behavior as a roller. Previous field research [29] showed that *G. sturmi* was very effective in dung removal, corroborating the results of the current study.

Onthophagus m. andalusicus also performed well in enriching the lower soil levels with organic matter and nutrients, despite a significantly lower rate of dung dispersion and use at the surface. The ability of this species to dig deeper tunnels could contribute to its efficiency in incorporating nutrients at greater depths. *Onthophagus vacca* and *E. crocatus* showed weaker performance, which could be due to slight variations in the depth of their burrows. Our results contrast with studies that suggest tunneling dung beetles play a more important role in dung removal compared with rollers and dwellers [37,38]. In the present study, overall, *G. sturmi* demonstrated higher performance in terms of dung removal and nutrient incorporation, highlighting the potential variability in dung beetle efficiency depending on species-specific behaviors and environmental context. A caveat on this finding is that the microcosm experimental environment likely forced the roller, *G. sturmi*, to behave more like a tunneler in that it could not roll balls away from the dung mass, thereby likely making its dung burial more concentrated and, therefore, more efficient.

In combination with body size, several morphological traits, such as head area and width, pronotum length and width, prothorax height and volume, and anterior and posterior tibia size, were positively related to dung removal, as reported by [39–42]. Larger dung beetles, such as *G. sturmi*, with features such as larger head size and width, as well as larger pronotal dimensions, were found to be more efficient at dung removal, supporting the findings that body size and morphology significantly influence dung beetle function.

The differences in results between the treatments with dung beetles and control treatments (dung only and no dung) underline the overall importance of dung beetles in soil fertilization and nutrient cycling. Maintaining and even enhancing the diversity of dung beetle communities, with their varied ecologies, is a key element in pasture management [43,44]. Our results are consistent with earlier studies that demonstrated the importance of dung beetles in contributing to soil nutrient levels [26]. Through dung relocation and dung burying activities, dung beetles influence the physical and chemical properties of soils [42], as well as their biological properties. For example, dung relocation and brood ball construction facilitate the activation of soil microorganisms involved in the nitrogen cycle [8,45]. By tunneling, dung beetles help to reduce soil compaction and increase soil aeration [6], facilitating nitrogen mineralization [46].

Dung relocation strategy determines where mineralization and nitrification take place: inside the dung pad, at the dung–soil interface (dweller species), or below the surface (tunnelers and rollers). Body size of dung beetles also affects the amount of dung removed; larger individuals dig larger holes and galleries, enhancing aerobic processes [42]. Nervo et al. [40] and Stanbrook et al. [47] reported a positive relationship between dung beetle size and the ability to influence nutrient recycling.

In the present study, *G. sturmi*, a roller beetle slightly larger than the other species, buried only one dung ball in the soil at a time, intended as food for a single offspring, but also scattered large quantities of dung on the surface, as reported by [29], whereas the tunneling *Onthophagus* and *Euonthophagus* species dug complex nests containing numerous small dung pellets intended for their offspring. Maldonado et al. [48] found that the presence of dung beetles led to a significant increase in the availability of soil nutrients, including nitrogen, ammonium, and phosphorus. Dung beetles also contribute significantly to the decomposition of organic matter, promoting the release of nutrients into the soil [30]. Plant growth is facilitated by dung beetle activity, which increases soil nutrient levels [7,10,11,26,49].

However, our study on three tunneling and one ball-rolling dung beetle species had limitations in that greenhouse and microcosm experiments cannot fully replicate the complex interactions between dung beetles and their environments under natural conditions. Additionally, the relatively short duration of this study would not have captured the incremental, long-term effects of dung beetle activities on soil fertility and organic matter levels. Moreover, the small sample sizes, timing constraints, and the use of relatively small containers for experimentation were other constraints that should be pointed out. Despite these limitations, it is important to note that this greenhouse microcosm study was complemented by field studies [27,29], which provided additional insights into the biology, ecology, and ethology of the four subject species in a semi-natural environment in Morocco in north-western Africa.

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Institutional Review Board Statement: This study was conducted in accordance with the Declaration of Helsinki and approved by the General Director of Office National de Sécurité Sanitaire des Produits Alimentaires (ONSSA), Rabat (Morocco) for the issuance of collection permits.

Data Availability Statement: The data presented in this study will be available on request from the first author (H.H.); they form part of the corpus of her PhD thesis.

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