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ARTICLE
Animal Ecology

Dung beetles, but not rodents, contribute to brown bear feces removal, disaggregation, and secondary seed dispersal

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Abstract

Seed dispersal by endozoochory is essential to plant dynamics, but once released in the feces, the seeds face a hostile environment that is not always favorable to germination. Indeed, feces may contain inhibitors, have high seed density, and be densely structured. However, feces visitors such as vertebrates and invertebrates may play an essential role in secondary seed dispersal (SSD) and can alleviate the chemical and physical constraints of the feces. Yet, their relative roles in the dispersal of small- and medium-sized seeds are not well documented. In this study, we designed a field experiment in the French Pyrénées mountains to disentangle the relative role of vertebrate and invertebrate on feces removal, disaggregation, and secondary dispersal of small- and medium-sized seeds. We thus used 30 brown bear (*Ursus arctos*) fresh feces and separated each of them into three sub-samples submitted to different treatments allowing total access of any visitor, access restricted to invertebrates, and no visitor access, respectively. We inserted eight raspberry (*Rubus idaeus*) and five blueberry (*Vaccinium myrtillus*) marked seeds in each sub-sample to assess SSD. In parallel, we used camera and pitfall traps to document the presence of vertebrate and invertebrate visitors, respectively. After ten days, we weighed the fecal matter remaining, counted the remaining seeds, and assessed the feces disaggregation based on visual examination and objective criteria. We observed a significant effect of invertebrates on feces removal, disaggregation, and secondary dispersal of both seed species. Vertebrates did not visit the feces. Dung beetles caught in pitfall traps appear as the main secondary seed dispersers and disaggregation agents in this area. We also pinpointed that diet composition and structure of brown bear feces affect dung beetle attraction and activities. Our study in a temperate mountainous area identifies dung beetles as key agents in the disaggregation of large feces and secondary dispersal of small- and medium-sized seeds, with no evidence of rodents. Diet composition and the fecal matter trapping the seeds affect seed fate by modulating dung beetle activity. By releasing variable fecal contents, omnivorous

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primary seed vectors have an even more complex effect on seed fate than expected.

KEYWORDS
diplochory, disaggregation agent, endozoochory, invertebrate, seed dispersal effectiveness, seed size, transport engineering, *Ursus arctos*, vertebrate

INTRODUCTION

Seed dispersal is a key ecological process mediated by a diversity of abiotic and biotic vectors that shape plant distribution and communities. Biotic vectors often enable long-distance and directional dispersal through zoochory (Beckman & Sullivan, 2023; Jordano, 2017; Nathan et al., 2008). Such dispersal enables plants to colonize new environments, to change elevational (Mendes et al., 2025; Naoe et al., 2016, 2019) and latitudinal (Nuñez et al., 2023) ranges, and to potentially escape unfavorable abiotic or biotic conditions (Beckman & Sullivan, 2023). Vectors including mammals (Baltzinger et al., 2019), frogs (Gould & Valdez, 2024), reptiles (Valido & Olesen, 2019), birds (Lovas-Kiss et al., 2018), and invertebrates (Martins et al., 2006) disperse seeds through epizoochory (e.g., attached on the fur or the hooves) and endozoochory (e.g., consumed and defecated). Unlike epizoochory, endozoochory involves critical phases with repercussions for seed viability and germinability, either positive or negative. The chewing process already represents an important filter that may alter or even destroy certain seeds, drawing the limit between seed predation and seed dispersal (Janzen, 1971). Once ingested, the seed ends up in the digestive tract. Gut passage can increase germinability by removing the pulp or conversely reduce seed viability. Coevolution between plants and animals selected seed traits favoring their resistance and adaptation to the animal digestive tract (Traveset et al., 2007; Traveset & Verdú, 2002). The journey is not over after digestion because seeds embedded in the feces have to cope with a harsh (Enders & Vander Wall, 2012; Pauly et al., 2024) but somewhat fertile environment (Traveset et al., 2007).

Frugivore or omnivore feces may contain a very high seed density, usually from different plant species, leading to competition and potential negative density-dependent or allelopathic effects (Traveset et al., 2007). Furthermore, feces is a complex matrix with both physical and chemical properties related to the animal diet (Frank et al., 2017; Ramos et al., 2024; Stricklan et al., 2020), which can influence fungi and bacteria development (Meyer & Witmer, 1998) and may reduce germination potential (Enders & Vander Wall, 2012; Pauly et al., 2024; Valenta & Fedigan, 2009). Indeed, feces are physically challenging (Mancilla-Leytón et al., 2012; Pauly et al., 2024) and may contain inhibitors (Malo & Suárez, 1995; Ramos et al., 2024; Traveset et al., 2001), affecting germination in the end. Among endozoochorous agents, large mammals appear to release an even more unfavorable feces environment for seed germination with exacerbated constraints. For instance, Stricklan et al. (2020) show that small and porous bird poops do not hamper germination in contrast to larger and thicker mammal feces, which is in agreement with other monospecific studies (Mancilla-Leytón et al., 2012; Miller, 1995; Pauly et al., 2024). However, once seeds germinate, feces may provide a fertile environment favoring seedlings' growth (Traveset et al., 2007 but see Miller, 1995, Pauly et al., 2024), though this effect may change among animal species (Ramos et al., 2024) or with intraspecific diet variation (Traveset et al., 2001). In this context, feces' visitors and disaggregation agents should play a key role in seed dispersal success by limiting these constraints through disaggregation and secondary seed dispersal (SSD or diplochory).

Visitors of mammal feces can remove and disaggregate part of the feces, reducing seed density within the feces and secondary disperse part of the seed pool (Lawson et al., 2012; Milotić et al., 2019; Niederhauser & Matlack, 2017; Urrea-Galeano et al., 2019). All of which globally increase seed dispersal effectiveness (Culot et al., 2015; Falcon et al., 2024; Ishikawa, 2011). Feces disaggregation and SSD agents are usually rodents (Culot et al., 2009; Pan et al., 2016; Wall et al., 2017), dung beetles (Andresen & Urrea-Galeano, 2022), or sometimes ants (Blanco et al., 2011; Böhning-Gaese et al., 1999; Bona et al., 2023). Rodents, attracted by the odor of the feces (Beaune et al., 2012), are interested in the large and numerous seeds contained in mammal feces that may represent an energetic banquet (Koike et al., 2012; Shakeri et al., 2018). In tropical areas, rodents are often considered seed predators and a threat to seed survival (Nichols et al., 2008) even if some reports involve scatter-hoarding behavior of viable seeds (Andresen, 2002; Forget & Milleron, 1991; Jansen et al., 2002). In temperate areas, however, rodents are better recognized for their role in SSD (Enders & Vander

Wall, 2012; Koike et al., 2012; Niederhauser & Matlack, 2017; Pan et al., 2016; Shakeri et al., 2018) than for seed predation (but see Bermejo et al., 1998; Koike et al., 2012; Pan et al., 2016).

Dung beetles are well-known to disaggregate feces (Milotić et al., 2019) and for their SSD function (Andresen & Urrea-Galeano, 2022; Milotić et al., 2019). They are primarily interested in the fecal matter regardless of the seeds it contains (Andresen & Urrea-Galeano, 2022). In fact, several factors can influence visits by dung beetles and SSD, as recently reviewed by Andresen and Urrea-Galeano (2022). For instance, the type and texture of feces may modulate the attraction of dung beetles due to specific stimuli like volatile organic compounds (Frank et al., 2017, 2018; Santos-Heredia et al., 2010). Therefore, depending on the animal diet and physiology, the feces may attract particular dung beetle functional groups in variable abundances (Andresen & Urrea-Galeano, 2022; Enari et al., 2016; Frank et al., 2017; Milotić et al., 2019; Noriega, 2012; Santos-Heredia et al., 2011). In this context, feces from omnivores such as brown bears may attract a community of dung beetles specific to herbivores and also carnivores (Frank et al., 2017) probably depending on omnivore feces composition. Variation in the dung beetle community induces different functions and roles for the seed fate (Griffiths et al., 2016; Manning et al., 2016; Milotić et al., 2019), which raises questions about the fate of seeds within the diverse feces omnivores release. Other factors such as the fecal deposition pattern (Fuzessy et al., 2022 but see Santos-Heredia et al., 2010), the defecation site (Santos-Heredia et al., 2011), or the amount of feces (Andresen & Urrea-Galeano, 2022) also modulate the feces attractivity of dung beetles and thus disaggregation and SSD. In fact, the seeds dispersed are usually smaller or equal to the size of the dung beetle, and seed shape or appendages may affect secondary dispersal probability (Andresen & Urrea-Galeano, 2022).

However, the relative role of vertebrates and invertebrates in seed fate from mammal feces has rarely been tested experimentally in sites when or where both are present (Culot et al., 2009; Hulme, 1997; Pan et al., 2016), especially in temperate areas (Koike et al., 2012). Furthermore, these few previous studies focused on large seeds (Hulme, 1997; Koike et al., 2012; Pan et al., 2016), and their findings cannot be applied to determine the relative contribution of vertebrates and invertebrates to smaller seeds secondarily dispersed. Small- and medium-sized seeds may interest rodents (Shakeri et al., 2018; Wall et al., 2017) and be easily transferred by dung beetles (Andresen & Urrea-Galeano, 2022; Milotić et al., 2019). We hypothesize that feces visitors can be significant agents on small- and medium-sized seed fate by removing part of the feces, by reducing the seed pool, or by disaggregating the fecal matrix (H1) and that both types of visitors are implicated in such a process (H2). As mentioned previously, the characteristics of the feces (e.g., amount, deposition site, composition, and release pattern) containing the seeds are critical for their detection and disaggregation. In this sense, omnivores that release feces composed of meat, plant, insect, or mixed items should induce variable seed fate. We hypothesize that for a given omnivore, the feces composition has a determinant effect on its attractivity, disaggregation, and SSD by biotic visitors (H3).

To test our first two hypotheses, we designed a realistic experiment (as suggested by Andresen & Urrea-Galeano, 2022) in a temperate area using feces of brown bear (*Ursus arctos*, L. 1758). Brown bear is an omnivore that consumes plants, insects, or meat (Lagalisse et al., 2003) and is well-known to disperse seeds of various sizes from fleshy-fruit-bearing plants as well as herbaceous plants (García-Rodríguez et al., 2021; Lalleroni et al., 2017; Pauly et al., 2024), thus making it a relevant biological model for studying these interactions in a temperate area. In our field experiment, we first assessed the relative effect of vertebrates and invertebrates on (1) feces removal, (2) feces disaggregation, and (3) small- and medium-sized seed secondary dispersal. At the same time, we identified the feces visitors using cameras and pitfall traps. Furthermore, we tested the effect of diet composition on visitor attractiveness and activity based on seed secondary dispersal.

MATERIALS AND METHODS

Study site

Our study was conducted in the Pyrénées mountains (36,600 km^2) shared between the south of France, Andorra, and the north of Spain, and peaking at 3404 m of altitude. Pyrénées host a wide diversity of plants, including endemics (Ninot et al., 2017), and several potential long-distance seed dispersers, among which are the brown bear, small carnivores (e.g., European pine marten *Martes martes*, L. 1758), wild ungulates (e.g., Red Deer *Cervus elaphus*, L. 1758; pyrenean chamois *Rupicapra pyrenaica*, L. 1758), and domestic ungulates (e.g., sheep *Ovis aries* L. 1758). Many dung beetles including endemics (Jay-Robert et al., 2003) are present. More precisely, we conducted our field experiment in Melles (Haute-Garonne, France), in an open and flat semi-natural grassland, at the edge of a forest, at 1400 m of altitude and within the Pyrenean brown bear current distribution range.

Study population and feces collection

The brown bear population in the Pyrénées includes at least 83 individuals in 2023 and is therefore classified critically endangered by IUCN. It is growing in numbers, benefitting from previous translocations of 11 Slovenian brown bear individuals (in 1996, 1997, 2006, 2016, and 2018). In 2023, the population range covered about 7100 km^2 from the east to the west of the Pyrénées (Sentilles et al., 2024). Based on coproscopic investigations, the Pyrenean brown bear's seasonal diet is composed mainly of forbs and ungulates (mostly scavenged) in spring, berries in summer, and hard mast in fall. Other mammals and invertebrates also contribute to its diet (Lagalisse et al., 2003).

We collected very fresh (from the day) wild brown bear feces in the Pyrénées between 2019 and 2023 using a scat detection dog (Sentilles et al., 2021), following spotting, depredation, or identified feeding sites. We selected 30 feces large enough to conduct the experiment, collected in spring, summer, and fall, resulting in different diet composition. The composition of each feces was determined based on visual investigation of undigested remains of the main food items (e.g., seeds and fruits for soft plants, fibrous parts for plants, exoskeleton for insects, hair and bones for vertebrates). The pool of feces thus included 8 feces composed mostly of fragmented hard mast, 7 composed of soft mast, and 12 composed of vegetative parts of plants. One was composed of vertebrate material, one of invertebrates, and the last one of honey wax. There were no "large seed" detected in the feces used (e.g., cherry or apple seeds). Feces were stored at −20°C before the experiment.

Experimental design

Our experiment was conducted during the late summer 2024 at the beginning of September in an open area at the edge of the forest. We defrosted and split each of the 30 feces samples into three 100-g sub-samples (i.e., 90 sub-samples). For each feces, we distributed the three sub-samples into three treatments: total access (no cage), access restricted to invertebrates (i.e., invertebrate access, thanks to a wide-mesh cage, mesh = 1.3 cm), and no access (fine-mesh cage, mesh = 0.1 cm), respectively (see Figure 1).

To test SSD and ensure the same number of seeds per treatment, we inserted homogeneously eight *Rubus idaeus* (L. 1753) seeds (medium size, 6.00 × 3.00 mm [Cappers et al., 2006]) and five *Vaccinium myrtillus* (L. 1753) seeds (small size, 1.50 × 0.25 mm [Cappers et al., 2006]) per sub-sample, in line with Milotić et al. (2019). Seeds were thus inserted inside each sub-sample ($n = 90$) for a total of 720 and 450 seeds, respectively. To avoid importing non-Pyrenean seeds, they were extracted from Pyrenean brown bear feces, not used in this specific experiment. All seeds were colored neon yellow using a forestry paint that is non-noxious, non-irritating, waterproof, temporary, and UV-resistant to facilitate recovery and extraction at the end of the experiment.

The 90 feces were thus randomly deposited directly on grass separated by 50 cm from each other in nine rows

FIGURE 1 Illustration of the treatments carried out on the feces, allowing access of vertebrates and invertebrates ("Total access," with no cage), access only of invertebrates ("Invertebrate access," wide-mesh cage, mesh = 1.3 cm), and no access of aboveground visitors ("No access," fine-mesh cage, mesh = 0.1 cm). Photo credit: Grégoire Pauly.

of 10 sub-samples. For each feces sample, the three sub-samples were associated with the three treatments. Each cage was firmly anchored in the ground to prevent passage between the ground and the base of the cage. No ground screen was installed.

We assessed the visiting small vertebrates using three camera traps located at two corners of the experimental design, and at a height of 40 cm, the third one covered another part of the experiment. Vertebrate identification on pictures was done by the authors. We assessed visiting insects using three black circular pitfall traps filled with water and one drop of washing-up. We placed a mesh roof onto which we deposited at the center a non-accessible but odorant brown bear feces composed of fleshy fruits that were not used in the experiment. The pitfall traps were set a few meters from the experiment and for the same duration as the experiment. Once the feces were brought back to the laboratory, if any insects were found in the feces, they were identified. Identification was done by one of the authors, an expert on coprophagous and coprophilous insects.

The experiment and traps were left during 10 days from 10 to 19 September 2024 with regular checks to ensure that the experiment was running properly. We installed an electric cattle fence around the experiment and the traps (12 × 10 m) to prevent potential disturbance by roaming megafauna and a rain gauge to monitor precipitation. We took a picture of each sub-sample at the beginning and the end of the experiment directly in the field.

In parallel to the experiment, we set aside ~20 g of each of the brown bear feces used for the experiment ($n = 30$) as a "ratio control." We dried this ratio control in an oven (60°C) until no more weight loss was observed to estimate its final dry mass. This allowed us to calculate the ratio between fresh and dry mass for each sample and thus estimate the initial dry mass of the fresh 100-g sub-sample (Appendix S1 for ratio details).

Feces measurements

At the end of the experiment, each sub-sample was collected, dried in an oven (60°C) in the same way as for the ratio control, and then weighed to determine the final dry matter. We determined the fecal removal by subtracting final from initial dry matter. In each sub-sample, we also counted the number of remaining colored *R. idaeus* and *V. myrtillus* seeds using a mortar to break up dry fragments, collecting seeds under a binocular magnifier, and deploying similar searching time per sub-sample of the same diet composition to estimate SSD. SSD is the number of seeds that were not recovered at the end of the experiment for each plant species tested.

Based on the final picture of each sub-sample ($n = 90$), we assess the disaggregation of feces based on objective and innovative criteria (and never used before) (Figure 2). "Intact" can be a single fecal unit with no obvious traces of invertebrate or vertebrate activity. "Disturbed" can be a single fecal unit with the presence of dung invertebrate/vertebrate activity (e.g., small holes) on part of the feces. Alternatively, it can also show a few more or less connected secondary fecal units. "Very disturbed" can be a single unit with the presence of dung invertebrate/vertebrate activity on several parts of the feces. Alternatively, there may be several more or less connected secondary fecal units (Figure 2). The disaggregation status was assessed by wildlife specialists ($n = 3$) and colleagues from our research laboratories ($n = 9$) in single blind based on a picture without information of the treatment. For a given picture, the most frequent assessment among observers was kept, and in the event of a tie, a consultation between authors was held to make a final decision.

To assess the effect of the main diet composition of feces on visits, we used cumulative numbers of seeds retrieved in treatments with access for visitors (total access and access restricted to invertebrates).

Data analysis

To test the relative effect of vertebrate and invertebrate visitors on feces removal, we performed a Gamma Generalized Linear Mixed Model (GLMM), dealing with positive values, using sub-sample final dry mass as the response variable, treatment as the explanatory variable, sample ID as a random factor, and sub-sample initial dry mass as a co-variate.

To test the relative effect of vertebrates and invertebrates on small- and medium-sized seed removal, we performed a Gamma GLMM, dealing with positive values, using the number of seeds per sub-sample as the response variable, treatment as the explanatory variable, and sample ID as a random factor. We ran a model for each plant species (*R. idaeus* and *V. myrtillus*). If, for a species, all the seeds were removed from at least one sub-sample (i.e., $n = 0$), then a Poisson GLMM was performed to analyze the seed removal for this species, dealing with counted data and zero values.

To test the effect of treatment on the fecal sub-sample disaggregation, we performed a χ^2 test of independence per pair of treatment (e.g., χ^2 test on feces with total access vs. feces with no access treatment). To compare the information obtained with the feces removal values and the disaggregation score, we carried out a Spearman correlation test.

To test the effect of diet composition on visits, we ran separate analyses for *R. idaeus* and *V. myrtillus* and only

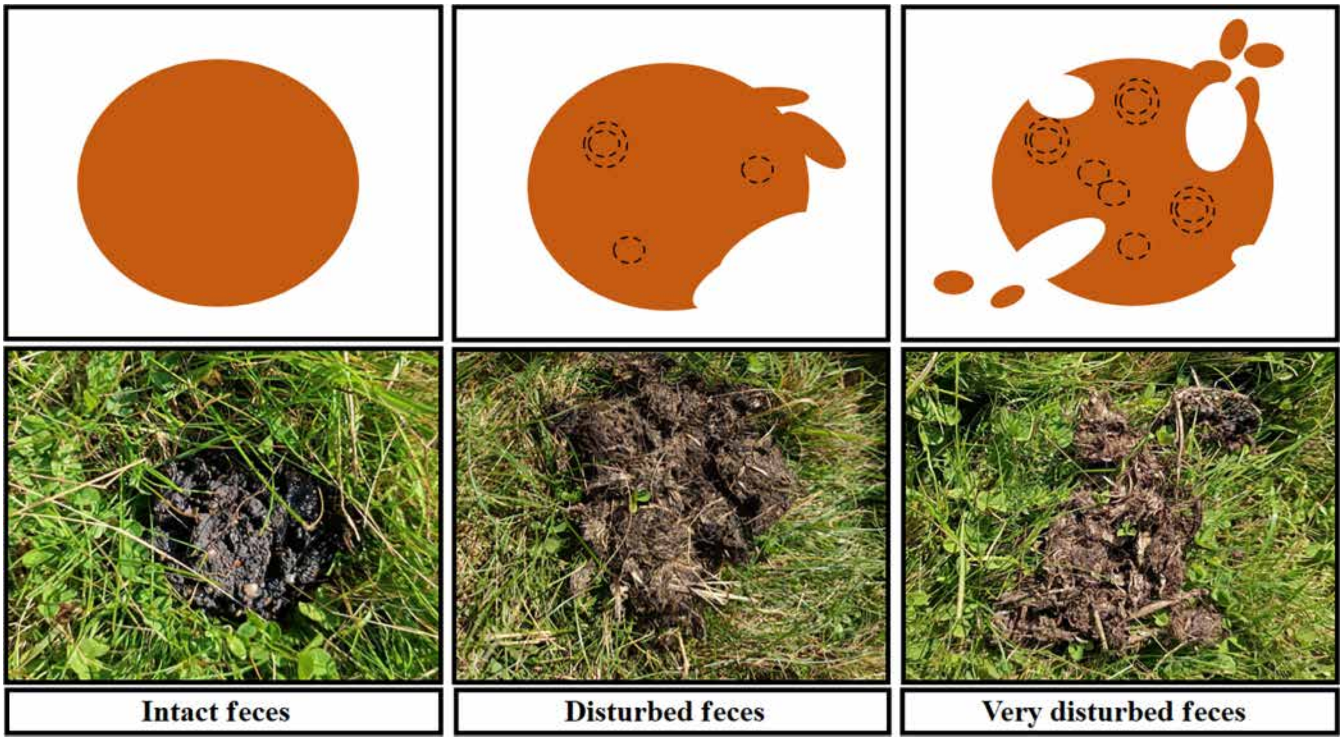

FIGURE 2 Schematic illustration and picture of feces according to the disaggregation assessment defined here: "Intact" feces show no clear evidence of visits by invertebrates or vertebrates. "Disturbed" feces show evidence of visits (holes, fragments). "Very disturbed" feces show numerous evidence of visits. Photo credit: Grégoire Pauly.

tested feces with diet composition that at least occurred twice: hard mast ($n = 8$), soft mast ($n = 7$), and vegetative plant parts ($n = 12$) as treatments. We discarded the other types of feces with a single occurrence (honey, meat, and insects). We performed a Gamma Generalized Linear Model (GLM), dealing with positive values, on the number of seeds with feces diet composition as an explanatory factor.

All the analyses were carried out in R studio (v. 4.3.3) using the lme4 package (v 1.1-35.5) (Bates et al., 2015) for GLM and GLMM. To obtain the marginal and conditional R^2 of our models, we used the MuMIn package (v. 1.48.4) and the trigamma method (Barton, 2024). The visualizations were carried out using Microsoft Office Professional Plus 2016 (Figures 1–2) and the ggplot2 package (v. 3.5.1) (Wickham, 2011) with R studio (Figures 3–5), keeping in mind color blind people. The silhouettes of dung beetles and rodents were freely obtained from Canva.

RESULTS

Feces removal

There was a significant effect of the treatment on feces material removal (Gamma GLMM, marginal $R^2 = 0.79$, conditional $R^2 = 0.88$, see Appendix S2 for details). Feces transfer was significantly higher in the sub-samples with total access of all visitors (7.3 ± 4.7 g; mean ± SD) than in the sub-samples with no access (5.2 ± 3.6 g; $p = 0.0002$, df = inf, z ratio = 3.995) and significantly higher in the sub-samples with invertebrate access only (6.8 ± 4.9 g) than in the sub-samples with no access ($p = 0.0422$, df = inf, z ratio = 2.410). We found no significant difference between sub-samples with total access of all visitors and sub-samples with invertebrate access only ($p = 0.250$, df = inf, z ratio = 1.590) (Figure 3).

Secondary seed dispersal

Seed extraction could not be carried out on the feces composed of honey due to the formation of an unbreakable paste after oven drying. We observed a significant difference in the number of *Rubus idaeus* seeds retrieved among treatments (Gamma GLMM, marginal $R^2 = 0.16$, conditional $R^2 = 0.31$, see Appendix S2 for details). Significantly fewer *R. idaeus* seeds were found at the end of the experiment in sub-samples with total access of all visitors (6.5 ± 1.9 seeds) than in sub-samples with no access (7.9 ± 0.3 seeds; $p = 0.0059$, df = inf, z ratio = −3.081), and in

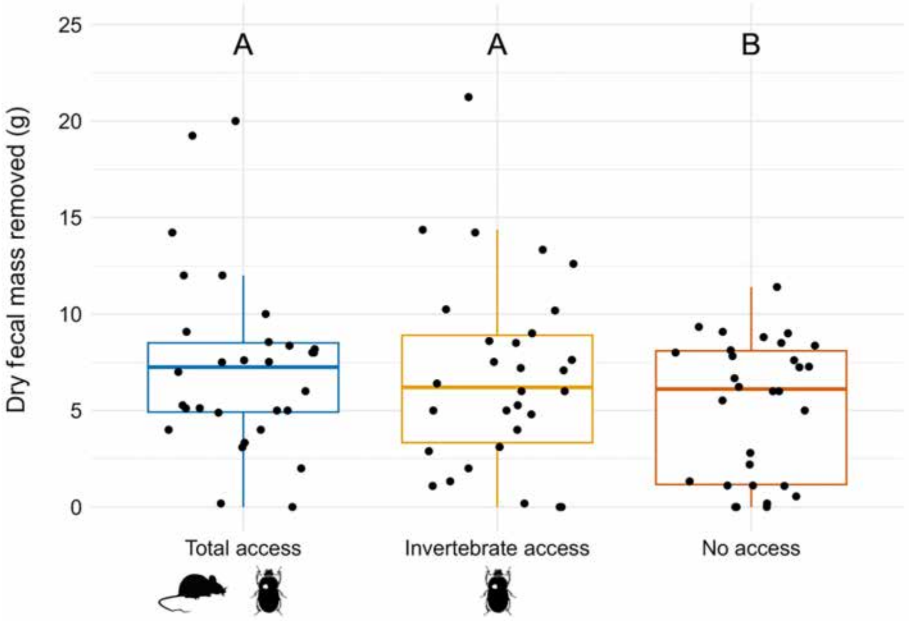

FIGURE 3 Boxplot (midline, median; box limits, quartiles; whiskers, maximum and minimum without outliers) of the dry fecal mass removed (measured as initial dry mass − final dry mass, symbolized by the points) from the sub-samples after 10 days in each treatment. Each treatment allowed access of vertebrates and invertebrates ("Total access"), invertebrates only ("Invertebrate access"), and no visitors from the surface ("No access"). The letters represent significant differences among treatments based on a General Linear Mixed Model (GLMM) Gamma.

sub-samples with invertebrate access only (6.3 ± 1.9 seeds) than in those with no access ($p = 0.0016$, df = inf, z ratio = −3.454). There was no significant difference in sub-samples with total access of all visitors and sub-samples with invertebrate access only ($p = 0.9235$, df = inf, z ratio = 0.380) (Figure 4). We observed a significant difference in the number of *V. myrtillus* seeds retrieved among treatments (Poisson GLM, marginal $R^2 = 0.11$; see Appendix S2 for details). Significantly fewer *V. myrtillus* seeds were found at the end of the experiment in sub-samples with invertebrate access only (2.7 ± 1.5 seeds) than sub-samples with no access (4.4 ± 0.6 seeds; $p = 0.0020$, df = inf, z ratio = −3.389). We observed no significant difference between sub-samples with total access of all visitors (3.3 ± 1.1 seeds) and sub-samples with invertebrate access only ($p = 0.3610$, df = inf, z ratio = 1.362) and a marginal difference between sub-samples with no access and sub-samples with total access of all visitors ($p = 0.0963$, df = inf, z ratio = −2.069; Figure 4).

Disaggregation assessment

The disaggregation assessment was done on the 90 sub-samples in blind by 12 people including the authors. Feces sub-samples with total access of all visitors and sub-samples with access restricted to invertebrates were assessed as "intact" with 7/30 and 7/30 occurrences each. Feces sub-samples with no access were assessed as "intact" in 15/30 occurrences (Table 1). We observed a significant difference in disaggregation between sub-samples with no access and sub-samples with total access of all visitors (χ^2 test, $\chi^2 = 9.3$, df = 2, $p = 0.010$) and between sub-samples with invertebrate access only and sub-samples with no access ($\chi^2 = 7.5$, df = 2, $p = 0.023$). We found no significant difference between sub-samples with no access and sub-samples with invertebrate access only ($\chi^2 = 0.4$, df = 2, $p = 0.826$). We found a weak correlation (Spearman correlation, 0.12) between disaggregation score and value of feces removal.

Effect of diet composition

The main food composition of the feces had an effect on *R. idaeus* removal (Poisson GLM $R^2 = 0.15$; see Appendix S2 for details) with significantly more seeds retrieved in feces composed of hard mast (15.1 ± 0.8 seeds) than in feces composed of vegetative parts (12.0 ± 3.1 seeds) ($p = 0.04$, $t = -2.181$). There was no significant difference in *R. idaeus* removal between feces composed of hard mast and feces composed of soft mast

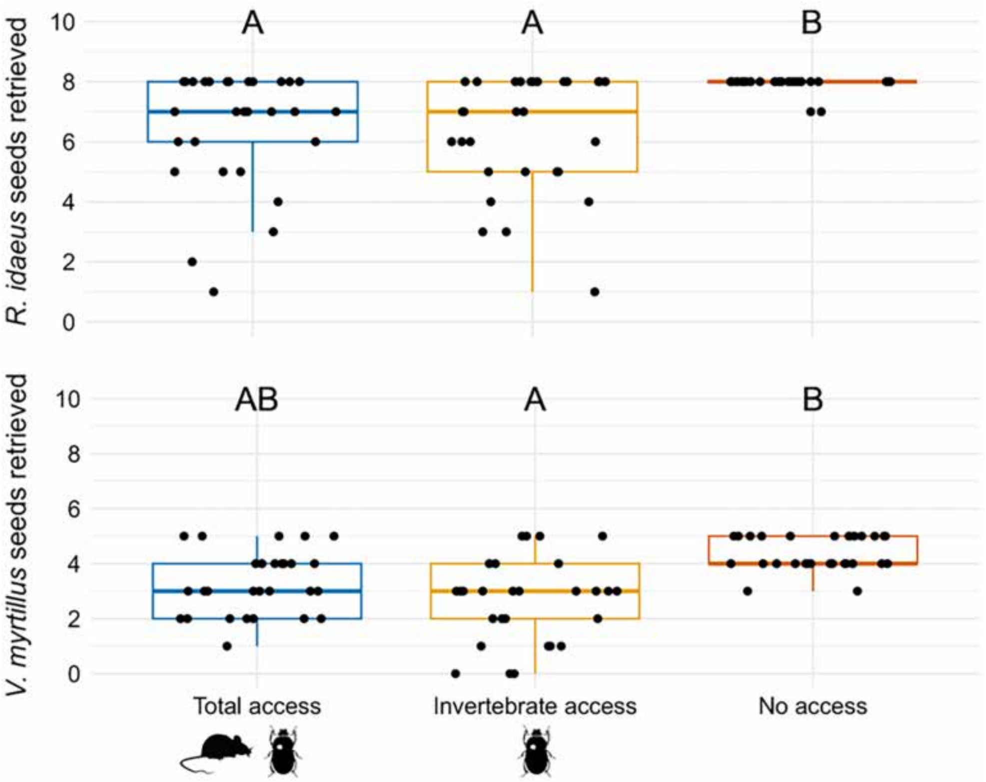

FIGURE 4 Boxplot (midline, median; box limits, quartiles; whiskers, maximum and minimum without outliers) of the number (points) of *Rubus idaeus* (initially $n = 8$) and *Vaccinium myrtillus* (initially $n = 5$) retrieved from feces sub-samples in each treatment. Each treatment allowed access of vertebrates and invertebrates ("Total access"), invertebrates only ("Invertebrate access"), and no visitors from the surface ("No access"). The letters related to the number of *R. idaeus* represent significant differences among treatments based on a General Linear Mixed Model (GLMM) Gamma. The letters related to the number of *V. myrtillus* represent significant differences among treatments based on a General Linear Model (GLM) Poisson.

TABLE 1 Feces disaggregation assessment of the 90 sub-samples performed by wildlife experts and scientists according to access of feces to vertebrate and invertebrate visitors (total access), invertebrates only (invertebrate access), and no aboveground visitors (no access).

	Total access		Invertebrate access		No access	
State of feces	No. sub-samples	Percentage	No. sub-samples	Percentage	No. sub-samples	Percentage
Intact	7	23	7	23	15	50
Disturbed	14	47	16	53	14	47
Very disturbed	9	30	7	23	1	3

Note: Each cell contains the number or percentage of sub-samples per state of faces for each type of access.

(12.7 ± 3.9 seeds), as well as between feces composed of soft mast and vegetative parts (Figure 5). We observed no significant differences (see Appendix S2 for details) in *V. myrtillus* removal among feces composed of hard mast (7.0 ± 1.9 seeds), soft mast (6.6 ± 1.5 seeds), and vegetative parts (6.7 ± 3.0 seeds) (Figure 5). In the feces composed mostly of meat, we retrieved 6/16 *R. idaeus* and 4/10 *V. myrtillus* seeds, while in the feces composed of insects, we retrieved 11/16 *R. idaeus* and 6/10 *V. myrtillus* seeds. We were not able to count seeds in the feces composed of honey.

Visitors community

No vertebrate visitors were detected with the camera traps during the experiment. The camera traps were frequently triggered during dung beetle flights. Based on pitfall traps and insects retrieved in feces, eight taxa of invertebrates were identified, including three dung beetles: two *Anoplotrupes stercorosus* (Scriba 1791), one *Trypocopris pyrenaeus* (Charpentier 1825), and four females of *Onthophagus* gr. *ovatus* (Latreille 1802). We also identified ground beetles (one *Calathus luctuosus*,

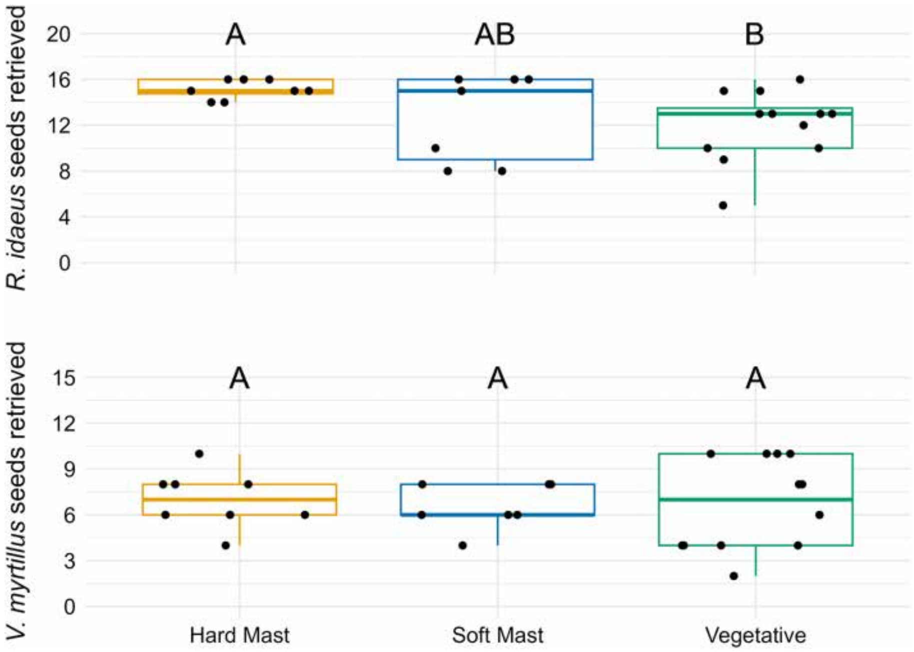

FIGURE 5 Boxplot (midline, median; box limits, quartiles; whiskers, maximum and minimum without outliers) of the number (points) of *Rubus idaeus* and *Vaccinium myrtillus* seeds counted in feces accessible to visitors (feces with total access or access restricted to invertebrates) according to the main diet composition: hard mast, soft mast, or vegetative parts. The letters in graphics represent the significant difference among main food compositions from a General Linear Model (GLM) Gamma.

Latreille 1804; one *Amara lunicollis*, Schiødte 1837), earwigs (six *Forficula auricularia*, L. 1758), and honey bees (nine *Apis mellifera*, L. 1758). The *Onthophagus* gr. *ovatus* was retrieved in feces after the end of experiment.

No disturbance of the experiment from humans or ungulates was reported. There was only one day of rain (September 11, 2024) with 14 mm measured with the rain gauge.

DISCUSSION

Our experiment in Pyrénées based on brown bear feces reveals the crucial role that visitors play as disaggregation agents (feces removal and disaggregation) and secondary seed dispersers of small- and medium-sized seeds, and how it is affected by the diet composition. Such activities are essential processes for limiting the constraints exerted by the feces matrix on seeds and improving their germination (Enders & Vander Wall, 2012; Pauly et al., 2024; Ramos et al., 2024). We observed significantly less feces material and seeds removed in feces with a fine-mesh cage, which prevented any visit from aboveground visitors, congruent with Koike et al. (2012) and our hypothesis H1. Based on few seeds inserted per sub-sample, we observed a significant activity of SSD by visitors in only 10 days, in agreement with (Milotić et al., 2019) on dung beetle SSD in Europe. It has been reported that such activity of feces visitors increases the seed dispersal effectiveness of primary seed dispersers with more seedlings observed (Culot et al., 2015; Falcon et al., 2024; Ishikawa, 2011). The disaggregation assessment, as objectively as possible, shows that feces accessible to visitors are more disaggregated than feces with no aboveground visitors, strengthening our other results and congruent with our hypothesis H1. However, part of the variation could also be due to handling bias or to our inability to collect the complete feces content and seeds even if we did this with a high degree of precaution. The loss of feces material or seeds in sub-samples with no access of aboveground visitors, and the similar percentage of disturbed feces between the three access treatments, can be due to abiotic factors, bacteria decomposition, soil biotic agents (Koike et al., 2012), or feces handling at the beginning or the end of the experiment. Furthermore, and contrary to our hypothesis H2, our study in temperate ecosystems reveals that invertebrates are the predominant SSD and disaggregation agents as we observed no vertebrates with camera traps and no difference between treatments with or without access of vertebrates (i.e., feces with no cage or with a wide-mesh cage) in feces removal, seed removal, and disaggregation assessment. Based on those findings, for constraining brown bear feces (Pauly et al., 2024) that may contain numerous seeds with strong competition among them

(García-Rodríguez et al., 2022), such activity by dung beetles might be crucial in the role of brown bears in seed dispersal (García-Rodríguez et al., 2021).

The invertebrates identified included three dung beetle species and a few other species (ground beetles, bees, and earwigs), while other potential agents such as maggots were not observed probably due to the time of the year (Sladecek et al., 2017). Dung beetles were the most numerous coprophagous group collected. The low abundance of insects collected may be explained by the attractiveness of brown bear feces (Frank et al., 2017) or by our monitoring to collect them. However, this suggests that dung beetles, which also frequently triggered camera traps, were the main invertebrate group of feces removal, disaggregation, and SSD in this study, which are organisms usually implicated in such processes (Andresen & Urrea-Galeano, 2022). The seeds were probably secondarily dispersed horizontally or vertically and buried in the soil seed bank (Andresen & Urrea-Galeano, 2022). Our results support previous findings on the effect of dung beetles in reducing seed aggregation within feces (Milotić et al., 2019; Santos-Heredia et al., 2010; Urrea-Galeano et al., 2019). Studies in tropical areas show also that such dispersal induces a decrease in seedling aggregation but also contrasting effects on the establishment of these seedlings, which depend on other biotic factors (Lawson et al., 2012; Urrea-Galeano et al., 2019). The short duration of our study also reveals that SSD and disaggregation can occur very quickly following feces release.

In this study, we also pinpointed that the composition of brown bear feces has a significant effect on visitor activity, here dung beetles, which is congruent with our hypothesis H3. Indeed, feces composed mostly of hard mast were significantly less visited than feces composed of soft mast or vegetative parts, and we observed important seed removal in the single feces composed of meat. This difference is probably due to the texture or the nutrients in the feces (Andresen & Urrea-Galeano, 2022; Frank et al., 2017) or may be related to the experimental design we used. The effect of feces composition on dung beetle's community and activity has been noticed previously within frugivore monkey species (Santos-Heredia et al., 2011) or among animal species with different diets (Enari et al., 2016; Frank et al., 2017). In this sense, seed fate may also depend on the fecal matrix in which seeds are embedded. For omnivores like the brown bear, feces composition is more variable than for frugivores, suggesting that the spectrum of effects of the fecal matrix on dung beetle community attraction (Frank et al., 2017) and the seed fate may be even wider. The effect of feces composition should be relevant for most of the omnivores involved in seed dispersal (e.g., Suids [Massei & Genov, 2004] or Mustelids [Otani, 2002; Tochigi et al., 2022]), with potential positive implications for dung beetle diversity.

Rodents, usual secondary seed dispersers (Culot et al., 2009; Pan et al., 2016; Wall et al., 2017), did not seem to be attracted by the small- and medium-sized seeds used in our experiment or by hard mast fragments, thus providing no effect on feces disaggregation or SSD. It contrasts with other studies showing that rodents are important feces visitors and secondary seed dispersers (Enders & Vander Wall, 2012; Koike et al., 2012; Pan et al., 2016; Shakeri et al., 2018). Although rodents can be attracted by medium-sized seeds (Shakeri et al., 2018; Wall et al., 2017), studies that unveiled such SSD activity focused on larger seeds such as *Prunus* sp. (L. 1753), *Cornus* sp. (L. 1758), *Taxus* sp. (L. 1753), or *Rhamnus* sp. (L. 1753) (Enders & Vander Wall, 2012; Koike et al., 2012; Pan et al., 2016; Shakeri et al., 2018). The feces may only be attractive to rodents when large seeds are present and visible, and small- or medium-sized seeds are only consumed from fruit or when they are available on the ground. The small number of seeds included may also explain the lack of attractiveness to rodents, although we did not observe any activity on feces initially composed of soft mast (*R. idaeus*, *V. myrtillus*). The site of our experiment (open area at the edge of a forest) may also explain these results, as the rodent community in temperate areas can be more species-rich inside forests (Shakeri et al., 2018). Another explanation can be the proximity of a hiking trail, which was potentially limiting rodent activity (Lee et al., 2019). However, brown bear can also transport large seeds (García-Rodríguez et al., 2021; Lalleroni et al., 2017) and may interest rodents (Shakeri et al., 2018).

Other vertebrates present in the Pyrénées, such as birds, can handle feces (e.g., *Pyrrhocorax pyrrhocorax*, *Upupa epops*, or *Milvus milvus*) (Niederhauser & Matlack, 2017; Young, 2015). For instance, *Upupa epops* can flip dry cow feces to collect insects beneath (Skead, 1950), whereas some birds such as *Eremophila alpestris* can break open the feces (Bent, 1942). In fact, other animals (e.g., mammals, amphibians, squamates, or other invertebrates) may interact with feces (Young, 2015). Interaction and disturbance by those dung beetle predators may have important effects on the fecal matrix and seed germination (Enders & Vander Wall, 2012; Pauly et al., 2024). Consequently, we argue that similar to carrion (Anderson, 2019; Bajerlein et al., 2011), feces may represent a trophic successional environment with coprophagous insects and then their predators (Koskela & Hanski, 1977), all potentially playing a role in feces decomposition and the fate of small- and medium-sized seeds in brown bear feces.

Our field study is the first to test experimentally the relative role of vertebrates and invertebrates on the secondary dispersal of medium- and small-sized seeds. To confirm our results, other similar realistic studies should be carried out in temperate or tropical areas. Furthermore, monitoring the fate of displaced seeds would also provide valuable information on the dynamics of small- and medium-sized seeds, as well as helping to better characterize the effect of SSD on the seed dispersal effectiveness of brown bear or other species. It has been studied on larger seed removal by both types of visitors (Koike et al., 2012) or in other studies on dung beetles SSD (Lawson et al., 2012; Urrea-Galeano et al., 2019). Our disaggregation assessment seems to complement the measurement of feces removal and represents a first quantification attempt, but the development of even more objective indicators to determine feces disaggregation (e.g., based on picture with same angle, distance, and light) is welcome if we want to better assess this overlooked but crucial aspect (Pauly et al., 2024).

Overall, our study in temperate areas highlighted the role of dung beetles in small- and medium-sized seed removal and feces disaggregation, whereas vertebrates did not forage such feces (i.e., lacking larger seeds). However, other vertebrates, especially predators of coprophagous insects, may play a role in feces disaggregation. Therefore, future research is encouraged to consider the trophic succession in feces to quantify the role of each visitor in fecal disaggregation and SSD. Furthermore, we proved that the composition diversity of omnivore feces affected visitor activity and thus SSD. In this sense, the role of omnivore in seed dispersal appears even more complex than previously thought, and further consideration should be given to the fecal matrix composition enveloping seeds.

AUTHOR CONTRIBUTIONS

Grégoire Pauly and Christophe Baltzinger conceptualize and design the experiment with the help of Cécile Vanpé, Mélanie Roy, Jérôme Sentilles, and Tanguy Daufresne. Grégoire Pauly, Jérôme Sentilles, and Christophe Baltzinger performed the experiment. Jean-David Chapelin-Viscardi identified the invertebrates collected. Grégoire Pauly carried out the statistical analysis and visualization with the help of Cécile Vanpé, Mélanie Roy, Christophe Baltzinger, and Tanguy Daufresne. Grégoire Pauly wrote the first draft of the paper; Grégoire Pauly, Cécile Vanpé, Mélanie Roy, Tanguy Daufresne, and Christophe Baltzinger wrote the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Pauly et al., 2025) are available from Data INRAE: https://doi.org/10.57745/KFWPNI.

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SUPPORTING INFORMATION

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

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