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RESEARCH ARTICLE

Sheep dung input enhances arthropod biomass and a threatened insectivorous bird: Experimental management for conservation

Margarita Reverter[1,2] | Juan Traba[1,2] | Adrián Barrero[1,2] | Daniel Bustillo-de la Rosa[1,2] | Julia Gómez-Catasús[1,2] | Julia Zurdo[1,2] | Cristian Pérez-Granados[1,3]

[1]Terrestrial Ecology Group (TEG-UAM), Department of Ecology, Autonomous University of Madrid, Madrid, Spain

[2]Centro de Investigación en Biodiversidad y Cambio Global, Autonomous University of Madrid, Madrid, Spain

[3]Biodiversity Management and Conservation Programme, Forest Science and Technology Center of Catalonia (CTFC), Lleida, Spain

Correspondence
Margarita Reverter
Email: margarita.reverter@uam.es

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Abstract

1. In recent decades, Europe has seen a notable decrease in extensive grazing by domestic livestock; endangering semi-natural open habitats; and impacting soil, vegetation, arthropods and insectivores.
2. Despite the known ecological consequences of grazing decline, little research has explored the role of sheep dung in influencing plant cover, arthropod biomass and higher trophic levels, such as insectivorous birds.
3. To address this gap, a 3-year study (2017–2019) was conducted in a Mediterranean shrub-steppe in central Spain. Two 10-hectare non-grazed experimental plots received different doses of sheep dung, while a grazed area served as a reference. Vegetation structure was assessed annually, arthropods were sampled six times per year and the breeding space use of a threatened insectivorous bird was estimated annually.
4. While dung input did not affect vegetation structure, it had short-term positive effects on some arthropods, particularly epigeous and coprophagous species. Additionally, the insectivorous bird increased its use of space in response to dung application, likely due to the rise in arthropod biomass, a critical food resource.
5. In areas where sheep grazing is declining, sheep dung inputs may serve as an effective short-term strategy to increase the biomass of specific arthropod groups, indirectly benefiting their predators. Further research is needed to assess long-term effects on arthropod communities and a wider range of insectivorous species, aiding conservation efforts in areas facing low grazing pressures.

KEYWORDS

coprophagous biomass, dung input, epigeous biomass, habitat management, sheep grazing, steppe bird

1 | INTRODUCTION

Semi-natural open habitats in Europe have been developed and maintained because of traditional human activities (Carboni et al., 2015), such as regular mowing, controlled burns and especially extensive livestock grazing (Leuschner & Ellenberg, 2017). The importance of livestock grazing in the maintenance of semi-natural open habitats (Mohamed et al., 2007) lies in its effects on vegetation, including seed dispersal (Traba et al., 2003), direct defoliation, trampling (Zhang et al., 2022) and reducing plant biomass avoiding shrub encroachment (Evans et al., 2015; Filazzola et al., 2020). This effect of grazing on vegetation depends on vegetation type and productivity (Torma et al., 2023). Furthermore, the intermediate disturbance hypothesis suggests that livestock grazing enhances biodiversity at intermediate levels by creating a patchy vegetation structure with certain bare ground coverage and promoting plant richness and diversity (Boch et al., 2019; Yuan et al., 2016). Grazing can also have a negative effect on arthropods through direct mortality caused by unintentional consuming or trampling (Gish et al., 2017), specifically foliar arthropods (Filazzola et al., 2020). Extensive grazing has also direct positive effects on arthropod biomass and abundance (Gómez-Catasús et al., 2023)—particularly for detritivores, predators and coprophagous arthropods (e.g. Benton et al., 2003; Filazzola et al., 2020; Møller, 2001; but see van Klink et al., 2015)—and indirectly influences both arthropod biomass, especially for foliar groups (van Klink et al., 2015) and diversity by the introduction of plant structural heterogeneity (Bosco et al., 2019; Zhu et al., 2012).

The input of organic matter via dung deposition is another important direct effect of grazing on open ecosystems. It increases water availability and soil fertility, particularly in terms of nitrogen and potassium (Peco et al., 2006), and it also produces changes in vegetation structure and composition, promoting grass and herbs (Olsen et al., 2021). Sheep dung has been positively linked not only to the abundance and diversity of coprophagous arthropods (Nichols et al., 2009) but also to other arthropod groups, such as grasshoppers (Jerrentrup et al., 2014). All these processes may have consequences on food availability and then on space use by insectivorous predators (Gómez-Catasús et al., 2023; Reverter et al., 2021; Šálek & Żmihorski, 2018), since arthropods are the main food resource for higher trophic levels (Schoenly, 1990), such as amphibians, reptiles, birds and mammals (Balbuena et al., 2023).

Despite the key role of traditional livestock grazing in maintaining semi-natural open habitats, extensive grazing has declined over the last decades in Europe (Prins & Gordon, 2008; Traba & Pérez-Granados, 2022). This disappearance is causing changes in vegetation structure and floristic composition (Olsen et al., 2021; Prévosto et al., 2011; but see van Klink et al., 2015), driving the landscape towards shrub and tree encroachment (Sanjuán et al., 2018), one of the main threats to semi-natural open habitats (Pykälä et al., 2005). Consequently, several management practices for the safeguarding of these habitats have been suggested and sometimes implemented, such as (i) controlled burns (Mohamed et al., 2007; Sharma et al., 2023; Valkó et al., 2014), (ii) removal of invasive plant species (Sharma et al., 2023), (iii) modification of plant structure by cutting and clear-cutting to avoid shrub encroachment and tree regeneration (Carboni et al., 2015) and (iv) herbivore inclusion/exclusion (Sharma et al., 2023; Su et al., 2023; Zheng et al., 2023). The maintenance and promotion of extensive grazing is the preferred action.

In addition, experimental dung input experiments have been conducted in open ecosystems, primarily in steppe regions in Asia. These studies assessed the impact of dung input on soil fertility and pH (Zhang et al., 2015), soil nitrogen supply (Zhou et al., 2022) and soil nutrient and vegetation (Hou et al., 2023; Liu et al., 2015; Sugiura et al., 1998). Similarly, the effect of dung input on soil fertility and carbon sequestration has been addressed in European arable steppes, with the aim of improving land productivity (Gamajunova et al., 2021; Wiesmeier et al., 2018). Although there are some studies that have evaluated the effect of dung on arthropods (Dittrich & Helden, 2012), no prior study has assessed the cascading effects of dung input on higher trophic levels, such as insectivorous bird species.

Here, we aim to improve the knowledge about how experimental dung input may alter vegetation and fauna dynamics. More specifically, this work aims to assess the immediate (after application) and short-term (1-year after) bottom-up cascading effects of an experimental input of sheep dung on plants, arthropods and birds, using a strict insectivorous steppe bird as a model species. We selected the Dupont's Lark (*Chersophilus duponti*) (Vieillot, 1824) as predator target species because it is a resident, territorial, steppe habitat specialist (Gómez-Catasús et al., 2019; Pérez-Granados, Serrano-Davies, et al., 2018) and a strict insectivorous bird, whose diet is mainly composed of beetles and spiders (Zurdo et al., 2024). Previous studies have found a positive relationship between arthropod abundance and space use of the species (Gómez-Catasús et al., 2019, 2023; Reverter et al., 2019, 2021), which suggests that the Dupont's Lark could be a good study model to assess the impact of dung input treatment on higher trophic levels. As a steppe habitat specialist, its presence in the experimental plots after dung application might be used as an indicator of the adequate habitat quality for insectivorous birds. The species is catalogued as 'endangered' in the Spanish legislation (BOE Orden TED/339/2023) and globally as vulnerable by IUCN (BirdLife International, 2020). To prevent two random points from falling within the same 50 × 50 m pixel in the kernel density estimate (KDE) analysis, a minimum distance of 50 m was maintained between each random point, and therefore, the results of this study might be useful for further management interventions.

We predict that (i) the experimental dung application will not lead to marked changes in shrub vegetation structure, due to its slow growth rate. However, an increase in the presence of nitrophilous herbaceous plants is predicted due to the input of nutrients; (ii) sheep dung will increase arthropod abundance, specifically coprophagous, although this effect will be temporary and will tend to decline with time after application (Grüebler et al., 2010; Møller, 2001); and

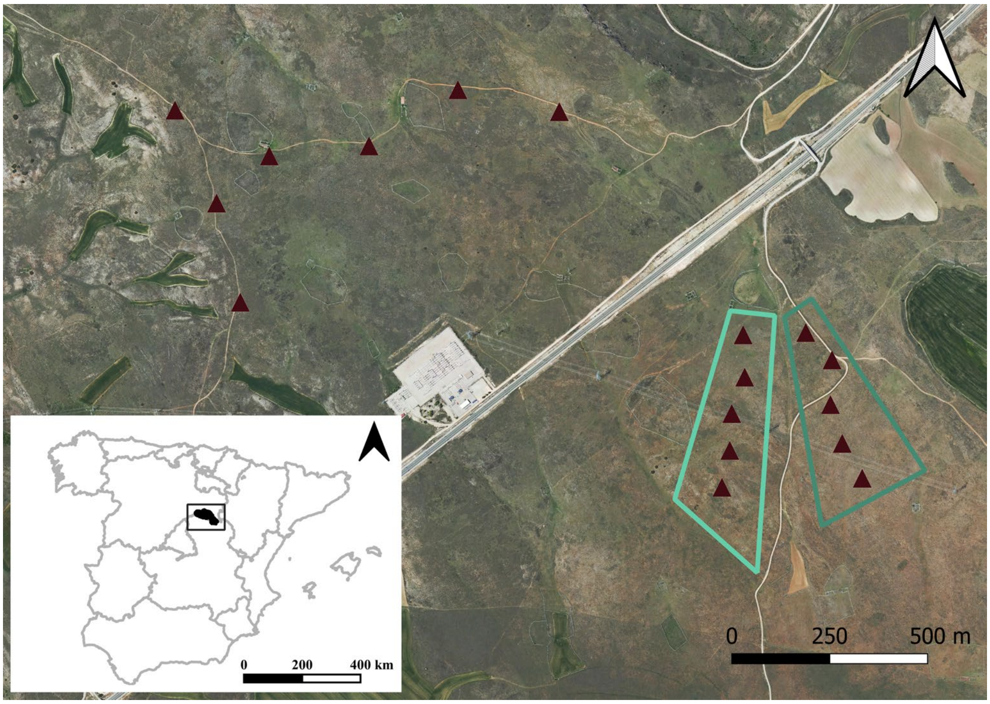

FIGURE 1 Location of the study area. The map illustrates the location of pitfall traps (brown triangles), as well as the reference area (upper left) and experimental plots (inside the polygons) differing between the high-density application (HDA, soft aquamarine, left polygon) and very high-density application of dung (VHDA, dark aquamarine, right polygon). The inset shows the location of the study area in Spain.

(iii) the expected increase in arthropod abundance should in turn be reflected in an increase in the use of space by insectivorous species.

2 | MATERIALS AND METHODS

2.1 | Study area

The experiment was carried out in a shrub-steppe of the Iberian Peninsula, which has the best representations of semi-natural open habitats in Western Europe, protected at European level due to the great diversity of flora and fauna that they hold (Zurdo et al., 2021). The study was conducted in Tierra de Medinaceli region, Soria province (central Spain; 41°11′N, 2°26′W, 1150 m a.s.l.; Figure 1), in an area of around 60 ha located in 'Páramos de Layna' special protection area (SPA ES4170120). Landscape is flat or gently undulated, dominated by a permanent short shrub-steppe (<40 cm height) of *Genista pumila*, *G. scorpius*, *Thymus* spp. and *Linum* spp., and a scarce grass cover of annual plants (Zurdo et al., 2021). Climate is continental Mediterranean, with a mean temperature of 10.6°C and a mean annual rainfall of 500 mm. There are some interspersed cereal fields and ploughings in the area.

An intense depopulation has taken place in the municipality of the study area (Medinaceli), which has been reduced by two-thirds from 1970 to 2016 (Pérez-Pérez-Granados, Serrano-Davies, et al., 2018). As a result, the study site and its surrounding SPAs have suffered intense land use changes in the last decades, from traditional extensive agriculture and livestock to agrarian intensification in a few productive spots (Alados et al., 2004; Garza & Traba, 2016; Gómez-Catasús et al., 2016), and a drastic reduction of grazing pressure or even abandonment in less productive marginal areas (Pérez-Granados, Serrano-Davies, et al., 2018).

2.2 | Sheep dung application design

We selected two experimental plots and one reference area (Figure 1). The selected experimental plots of 10 ha each were shrub-steppes visually similar to the reference area in terms of vegetation structure and gentle slope, where the livestock practice disappeared several years ago. The sheep dung input was arranged across the two experimental plots, each one with a different treatment: (1) high-density application (HDA) of sheep dung (=2500 kg ha^{-1}) and (2) very high-density application (VHDA) of sheep dung (=5000 kg ha^{-1}). A reference area (R) with no external input of sheep dung was also included (Figure 1). The upper left part of the map has a low grazing intensity by sheep (0.10–0.13 LSU/ha, Gómez-Catasús et al., 2023), while in the experimental plots and surroundings (south sector, Figure 1), there is no presence of livestock. The applied amount of dung in the HDA polygon (2500 kg ha^{-1}) simulates the excrement produced by a stocking rate three times higher than the mean stocking rate of the study area during the monitored period (Gómez-Catasús et al., 2023), while VHDA simulates a stocking rate six times higher than the current during the monitored period. For extended explanation about calculations of the amount of excrement produced by a traditional sheep herd per hectare and day, see Supporting Information S1.

Toxicological and heavy metals analyses were carried out to certify that the dung could be applied, following Spanish regulations. Dung input was carried out in April 2018, spreading in a trailer with a capacity of 12 t, with vertical cylinders and a basal conveyor belt, pulled by a 140-hp tractor with wide wheels or a rubber chain. Spreading prevented dung accumulation, generating a very thin, discontinuous layer of excrement (Supporting Information S2).

This study was conducted under the necessary permits granted by the Regional Government of Castilla y León (Department of Development and Environment, General Directorate of Natural Environment), under permit numbers EP/CyL/332/2017 and AUES/CYL/191/2020 (the latter being a special permit issued for the COVID period).

2.3 | Sampling stations

We located 17 sampling stations in areas with a slope <15% and dominated by permanent short shrub (<40 cm height). Ten of the sampling stations were in the experimental plots (5 in HDA, 5 in VHDA), while seven sampling stations were placed in the reference area. Sampling stations were separated by a minimum distance of 100 m between them. Each sampling station consisted of three sampling points placed at 5-m intervals (Figure 2).

2.3.1 | Vegetation structure coverage

At each sampling station, we conducted one vegetation sampling per year in spring during 2017 (previous to dung application, only in the reference area) and 2018 and 2019 (both after dung application, and in the reference area and experimental plots). In each sampling point, cover of overall vegetation, shrubs, herbaceous plants, detritus, rock, mosses, lichens and bare soil was visually estimated in a 1 × 1-m quadrat (Figure 2; see Gómez-Catasús et al., 2019; Zurdo et al., 2021 for a similar approach). Mosses and lichens were measured but finally excluded for further analyses due to the high variability associated with rapid responses after rain events. Covers were measured independently, so they may overlap and add up to covers greater than 100%. Vegetation structure coverage variables were *arcsin* transformed to achieve the requirements of normality and homoscedasticity (Siegel & Morgan, 1996).

2.3.2 | Arthropod biomass sampling

Arthropods were collected six times a year (January or February, April, May, June, July and September or October) in 2017 (prior to dung application), 2018 (first year after application) and three times in 2019 (January, April and May; second year after application). The choice of January/February and September/October sampling depended on weather conditions to avoid rainy days and ensure proper sampling. At each sampling point, three pitfall traps were placed to collect the epigeous community (51 pitfall traps per survey). Pitfall traps were transparent plastic cups (220 mL; 70 mm diameter, 100 mm depth, Figure 2) filled with 120 mL of 40% ethylene glycol and a drop of liquid soap to reduce surface tension (Schmidt et al., 2006). After a week, epigeous arthropods were collected and stored in plastic tubs with 70% ethanol. All stations were sampled on the same dates within each period (specific dates when arthropods were collected can be found in Supporting Information S3). At the moment of collecting pitfall traps, one person collected flying arthropods or those found on plants (for which pitfall traps are not a suitable sampling method) with a sweep net walking transect along the longest distance between pitfall traps (10 × 2 m band) and using a standardized zigzag movement along the transect. This combined system has been proven to be an effective method for the capture of a broad spectrum of epigeous and flying arthropods (Gómez-Catasús et al., 2019; Traba et al., 2007).

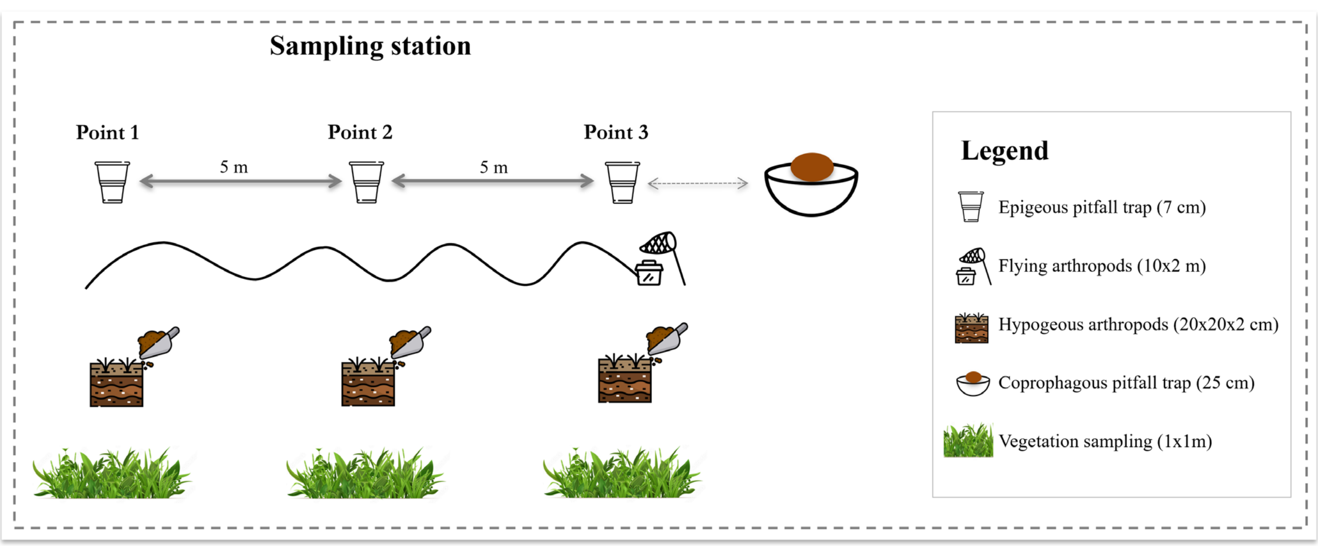

FIGURE 2 Sampling station outline. Each sampling station consisted of three sampling points.

Coprophagous arthropods were sampled with one pitfall trap per sampling station using 200 g of fresh sheep dung provided by local farmers as bait. The dung was placed in the centre of the trap on an elevated structure. This way, the faeces were surrounded by a mixture of ethylene glycol, but without direct contact with the liquid. The traps were collected after 24 h. Only those arthropods considered as coprophagous were identified from the coprophagous pitfall traps: order Coleoptera, family Scarabaeidae (Gymnopleurus spp., Onthophagus spp. and Scarabeus spp.); and order Diptera, suborder Brachycera, due to the importance of these groups in the diet of the study species, the Dupont's lark. Finally, the biomass of hypogeous arthropods was measured in soil samples of 20 × 20 and 2 cm depth taken next to the pitfall traps. Samples were stored in plastic bags and arthropods were sieved and identified within 48 h to prevent degradation. Oligochaetes (Phylum Annelida) were identified due to their importance in the diet of steppe birds because some studies highlight their importance in steppe birds' diet (Buchanan et al., 2006), including the Dupont's lark (Zurdo et al., 2023).

Arthropods were identified in the laboratory, taking as an operational taxonomic unit (OTU) the order level for all taxa, except for Coleoptera, which were identified to family or species level. To obtain biomass for each group of arthropods, we apply the Hódar-specific equations (Hódar, 1996) after measuring the corporal length of specimens, excluding legs, antennae and other appendices. For oligochaetes, we applied the biomass equation proposed by Collins (1992). In each sampling period, biomass per OTU was calculated as the mean values per station, except in the case of coprophagous biomass since only one sampling point was located per station (Gómez-Catasús et al., 2019). We only incorporated to the analyses those arthropod groups with a mean contribution equal to or higher than 4% of the total biomass collected. Due to the high proportion of ants found in the samples, the family Formicidae (order Hymenoptera) was considered as an independent group.

2.4 | Bird space use

We carried out Dupont's lark censuses by applying the mapping method (Pérez-Granados & López-Iborra, 2017) during the breeding period (April, May and June), both before (2017) and after (2018 and 2019) the dung experiment. Two 2-km transects were established, covering experimental plots and surroundings, with a 500-m detection band per side, considering the species' songs are audible up to 1500 m (Laiolo et al., 2007; Vögeli et al., 2010). Censuses were performed during Dupont's Lark peak of activity (1–1.5 h before dawn; Pérez-Granados, Osiejuk, et al., 2018) and spanned around 1 h. Singing males were mapped by georeferencing with GPS (GPS error ± 5 m). Each transect was repeated three times during the breeding season, alternating the starting point with the aim of registering the maximum singing activity in the species throughout the censuses. The number of breeding males was estimated by the mapping method, delimiting territories by gathering accumulated observations from different surveys and calculating the mean centroid (see Pérez-Granados & López-Iborra, 2017 for a detailed description of the counting method).

Finally, the intensity of space use by the Dupont's Lark during the 3 years of the study was calculated by means of a kernel density estimation (KDE). KDE was conducted separately for each year (2017, 2018 and 2019) employing the locations of Dupont's Lark male territories within and in the immediate surroundings of the experimental plots. KDE gives higher probability values to those areas with a greater number of points (bird territories in this case), adjusting the assigned values depending on the smoothing parameter (Worton, 1989). We estimated a KDE for each year using the kernel density estimation function of SAGA, in QGis 2.18 (QGis Development Team, 2017) with a smoothing factor of 600 m in accordance with Dupont's Lark maximum home range (up to 37.3 ha, Garza et al., 2005) and using a 50 × 50 m pixel (see Gómez-Catasús et al., 2023 for a similar approach and KDE estimation). To assess whether space use of the Dupont's Lark varied according to sheep dung input, we generated random points within the experimental plots and in a 500-m buffer around them (surroundings), avoiding non-optimal habitats for the species (crops, infrastructures, see Supporting Information S4). We considered a 500-m buffer because we only expected that sheep dung input may positively influence Dupont's larks inhabiting close to the experimental areas and because this distance is within the typical breeding dispersal movements of the species (Laiolo et al., 2007; Pérez-Granados et al., 2022). We extracted the values of intensity of space use (probability) for each point (HDA $N = 50$, VHDA $N = 50$, surroundings (S) $N = 661$, Supporting Information S4) in each year using the point sampling tool implemented in Qgis 2.18.28.

2.5 | Statistical analysis

Linear mixed models (LMMs) were chosen as they handle hierarchical data structures by incorporating random effects (e.g. sampling station and month). This approach accounts for dependencies in the data and provides accurate estimates of fixed effects.

First, we compared the changes in vegetation structure and arthropod variables in the reference area between years to evaluate whether there were natural (i.e. inter-annual) fluctuations during the study period. At the vegetation level, we fitted independent linear mixed models (LMMs hereafter), with a Gaussian error structure, considering each vegetation variable as a response variable: shrub cover, herbaceous cover, detritus cover, rock cover and bare ground cover. In the LMMs, *Year* (2017, 2018, 2019) was included as a fixed predictor, using the year 2017 as the reference value and the *sampling station* was considered as a random factor. Similar models were fitted to assess changes in arthropod biomass over time using the biomass of epigeous, hypogeous and coprophagous as response variables (three independent LMMs) and *Year* (2017, 2018, 2019) as a fixed predictor and *sampling station* and *sampling month* as random factors.

Second, we built LMMs to evaluate the effects of dung input on vegetation structure using as response variable each vegetation variable (shrub cover, grass cover, detritus cover, rock cover and bare ground cover), and *Year* (2018, 2019; 2018 used as reference value), *Action* (R, HDA, VHDA; R used as reference value) and the interaction between both factors as fixed predictors. *Sampling station* was considered a random factor. Again, similar models were fitted for the three arthropod groups (epigeous, hypogeous and coprophagous), but adding *sampling month* as a random factor. To facilitate the understanding of the results, the main text shows the effect of dung input on the three main functional groups considered in the study (epigeous, hypogeous and coprophagous), while the results by taxonomic groups can be consulted in the Supporting Information S5. Finally, we ran a linear model using the values of intensity of space use by the Dupont's Lark as response variable, and *Year* (2017, 2018, 2019; 2017 values as reference), *Action* (R, HDA, VHDA; R as a reference) and their interaction as explanatory variables. The linear model was run in a loop with 1000 iterations, using the same 50 points for each experimental plot and 50 different points for the surrounding area that changed randomly in each iteration. We estimated the mean, SD and 95% confidence interval (95% CI) from the 1000 iterations and considered predictors to influence the response variable when the parameter's 95% CI did not overlap zero.

3 | RESULTS

3.1 | Vegetation structure

In the reference area, there were no differences in shrub and rock cover among years (Table 1). However, when compared to 2017 values, herbaceous cover was significantly higher during 2018 (estimate = 0.191, df = 12.781, $t = 3.288$, $p = 0.006$); detritus cover was significantly lower during 2019 (estimate = −0.142, df = 11.524, $t = -3.907$, $p = 0.002$) and bare ground cover was significantly higher in 2018 (estimate = 0.148, df = 13.122, $t = 2.339$, $p = 0.036$) and significantly lower in 2019 (estimate = −0.162, df = 13.122, $t = -2.566$, $p = 0.023$, Table 1).

No effect of sheep dung inputs was observed on any of the vegetation structure variables considered, with shrub cover, herbaceous cover, detritus cover, rock cover and bare ground cover similar in the reference area and experimental plots (Supporting Information S6). Interannual differences in the dung input plots were detected: shrub cover was significantly higher in 2019 (estimate = 6.676, df = 14.00, $t = 2.196$, $p = 0.045$), while detritus and bare ground cover were significantly lower during 2019 (detritus: estimate = −5.180, df = 14.00, $t = -2.898$, $p = 0.012$; bare ground: estimate = −17.963, df = 14.00, $t = -5.919$, $p < 0.001$). Cover percentages can be consulted in Supporting Information S6.

3.2 | Arthropods

Over 45,000 arthropod specimens were identified during the 3 years of study (see detailed results in Supporting Information S7). In the reference area, the biomass of epigeous arthropods showed interannual variation, as they were significantly higher in 2018 than in 2017 (estimate = 286.240, df = 104.02, $t = 2.383$, $p = 0.019$). On the contrary, the biomass of coprophagous arthropods was significantly lower in 2018 (2018: estimate = −556.880, df = 89.92, $t = -3.413$, $p < 0.001$) and marginally significant lower in 2019 (estimate = −350.620, df = 88.58, $t = -1.969$, $p = 0.053$) when compared to 2017 values. The biomass of hypogeous arthropods did not differ significantly between years (Table 2).

When analysing the effect of treatment, HDA had a positive and significant effect on epigeous arthropod biomass (estimate = 600.840, df = 36.544, $t = 3.461$, $p = 0.001$, Figures 3 and 4), while VHDA had a marginally positive effect (estimate = 293.220, df = 36.544, $t = 1.689$, $p = 0.099$, Figures 3 and 4). This effect did not differ between years.

These effects differed depending on the taxonomic arthropod group analysed. The main order showing differences between experimental plots and the reference area was Coleoptera (see Supporting Information S5).

Dung input had no effect on either the abundance or biomass of hypogeous arthropods (see Supporting Information S7). Coprophagous biomass was significantly higher in VHDA (estimate = 73.344, df = 122.789, $t = 2.044$, $p = 0.043$, Figures 5 and 6) and HDA plots (estimate = 83.981, df = 122.789, $t = 2.341$, $p = 0.021$,

TABLE 2 Mean ± standard error (in mg) of epigeous, hypogeous and coprophagous arthropod biomass in the reference area in 2017, 2018 and 2019.

Year	Epigeous	Hypogeous	Coprophagous
2017	335.36 ± 44.00	0.08 ± 0.02	552.19 ± 356.15
2018	**825.70 ± 426.90**	2.13 ± 1.98	**84.57 ± 70.52**
2019	395.85 ± 325.68	2.43 ± 2.64	307.60 ± 276.88

Note: Treatments with significant differences between years, according to linear mixed models, are indicated in bold.

TABLE 1 Mean ± standard error cover (in percentage) of vegetation structure variables in reference areas in 2017, 2018 and 2019.

Year	Shrub	Herbaceous	Detritus	Rock	Bare ground
2017	37.75 ± 7.62	26.96 ± 4.16	9.63 ± 2.14	5.83 ± 2.40	12.08 ± 4.27
2018	30.00 ± 3.87	**45.29 ± 5.29**	6.33 ± 1.05	5.00 ± 1.54	**23.81 ± 9.00**
2019	40.95 ± 5.24	32.86 ± 6.01	**2.95 ± 1.09**	5.38 ± 1.74	**4.86 ± 1.84**

Note: Treatments with significant differences between years, according to linear mixed models, are indicated in bold.

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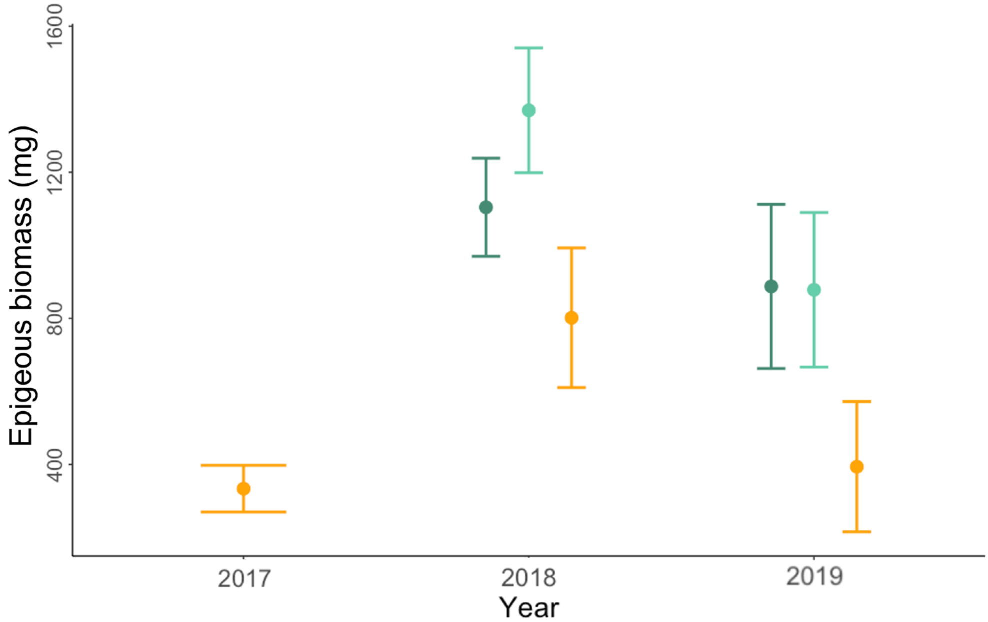

FIGURE 3 Mean ± SE of epigeous arthropod biomass per year in the reference area and experimental plots. Reference: Orange, VHDA: Dark aquamarine; HDA: Soft aquamarine.

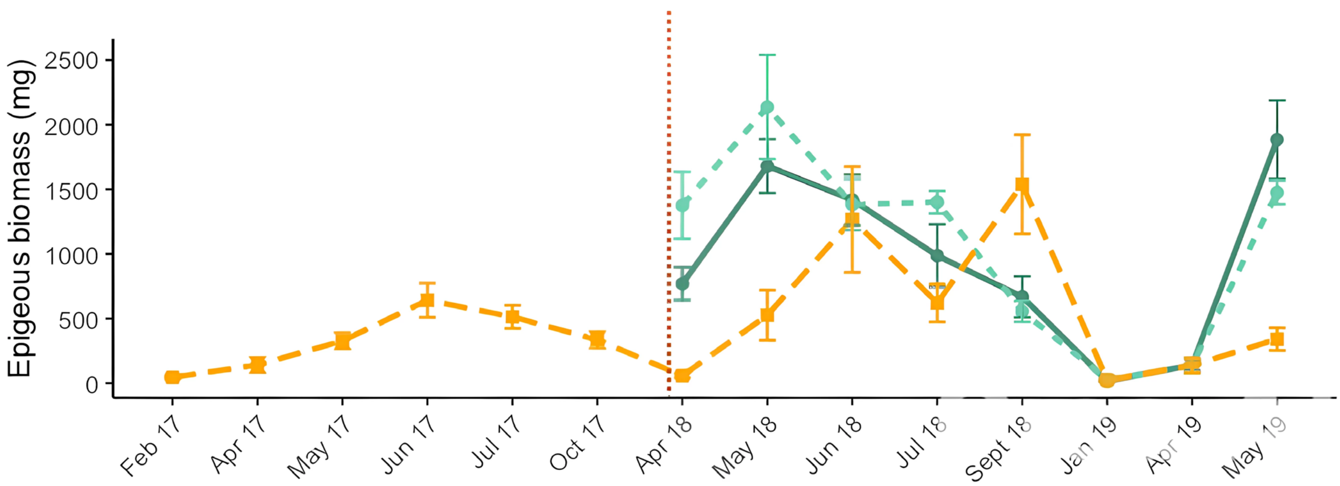

FIGURE 4 Mean ± SE of epigeous arthropod biomass per month in the reference area and experimental plots. Reference: Orange, VHDA: Dark aquamarine; HDA: Soft aquamarine. Brown dotted line indicates the dung input date.

Figures 5 and 6) than in the reference area, and this effect did not differ between years. Indeed, a consistent pattern of increasing epigeous and coprophagous biomass during the first spring after dung application comparing with the reference area was observed (Figures 4 and 6).

3.3 | Cascading effects of dung application on insectivorous species

The space use of Dupont's Lark was significantly lower during 2018 and 2019 than in 2017 in both the surroundings and experimental plots. The space use of the species was significantly higher in the experimental plots after the dung input (Table 3, Supporting Information S8). Specifically, VHDA had a positive effect on Dupont's Lark space use during 2018 (Table 3), while HDA had a positive effect on the space use of the species during 2018 and 2019 (Table 3).

4 | DISCUSSION

Our results suggest that sheep dung input may be useful as a management tool for improving several ecosystem attributes in

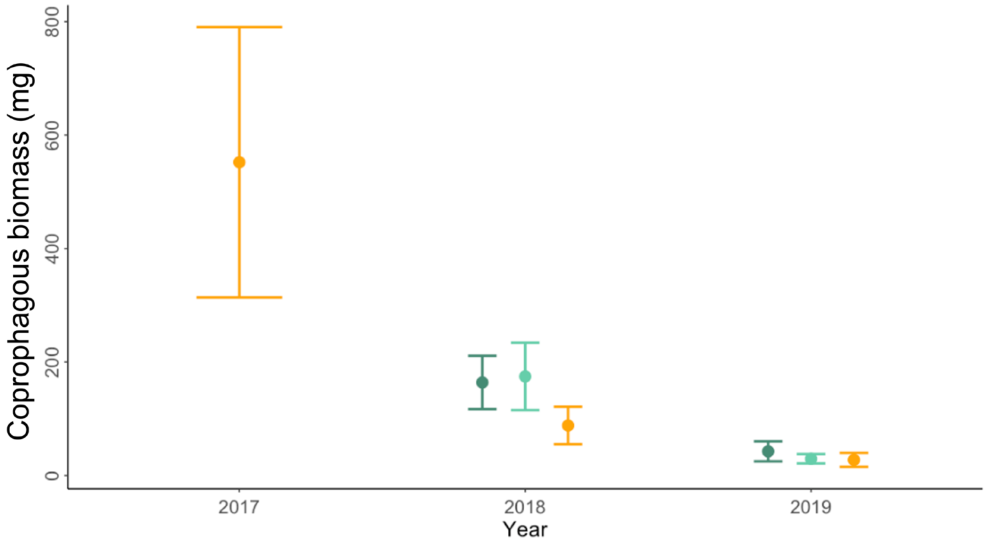

FIGURE 5 Mean ± SE of coprophagous arthropod biomass per year in the reference area and experimental plots. Reference: Orange, VHDA: Dark aquamarine; HDA: Soft aquamarine.

shrub-steppes linked to grazing, but its effects are short term. Sheep dung input did not alter habitat structure but had significant positive short-term effects on epigeous and coprophagous biomass. More specifically, dung input increased the biomass of non-coprophagous beetles, as well as that of coprophagous beetles and flies. Finally, sheep dung input showed positive effects on higher trophic levels by increasing the space use of an insectivorous bird in experimental plots. While we acknowledge that our data are pseudoreplicated due to multiple measurements per sampling station, we accounted for this by including *Sampling station* as a random factor in our model. Thus, we believe that the main conclusions regarding the positive impact of dung input on arthropod biomass and on Dupont's lark remain valid. We encourage future research on this topic to employ replicated designs to further validate the observed trends.

4.1 | Effects of sheep dung input on vegetation

Most of the vegetation variables measured did not vary over time, neither in the reference area nor in the experimental plots, which is probably due to the slow vegetation growth rate in the study area. This is consistent with prior research in the study area, which found only slight variations in shrub cover between years (Pérez-Granados, Serrano-Davies, et al., 2018). The lower detritus cover in 2019 in the reference area suggests higher soil microbial activity, possibly aiding in the decomposition of greater herbaceous cover observed in 2018 (Oggioni et al., 2020). Previous research in steppes showed that, in plots with higher herbaceous cover, the abundance of soil bacteria increased (Liu et al., 2015), possibly explaining this finding. Inter-annual differences in herbaceous cover in the reference area may respond to natural changes influenced by environmental variability (i.e. temperature and rainfall).

The application of sheep dung apparently did not affect the measured variables of vegetation structure during short-term monitoring, indicating its potential as a conservation measure to enhance arthropod abundance in semi-natural open habitats. The study's results support previous findings indicating that dung from small herbivores like sheep contains higher proportions of essential elements (C, N and P) for plants and animals compared to that of larger herbivores such as cows and horses. Larger herbivores contribute more to soil nitrification, potentially altering ecosystem structure and favouring nitrophilous species (Barbero-Palacios et al., 2023). The lack of impact on habitat structure aligns with our expectations, except for herbaceous cover. Contrary to expectations based on previous studies, herbaceous cover did not increase after dung application in the short term despite the potential presence of a seed bank within it (Oveisi et al., 2021), where a positive effect on herbaceous cover from dung application might be expected (Wang et al., 2019). However, recent studies in calcareous grasslands indicate that viable seeds in sheep dung samples are rare (Kuiters & Huiskes, 2010), which may partly contribute to explain our findings. Additionally, the dung spreading technique used in the study caused minimal disturbance to the habitat, making it a practical management approach. Nevertheless, studies focused on analysing potential long-term changes in vegetation structure should be conducted, as vegetation may take longer to respond to management changes (Perner & Malt, 2003).

4.2 | Effects of sheep dung input on arthropods

We found that epigeous arthropod biomass in the reference area was significantly higher in 2018 than in 2017, while coprophagous biomass decreased during the same period. Although invertebrate abundance can vary strongly between years, one possible

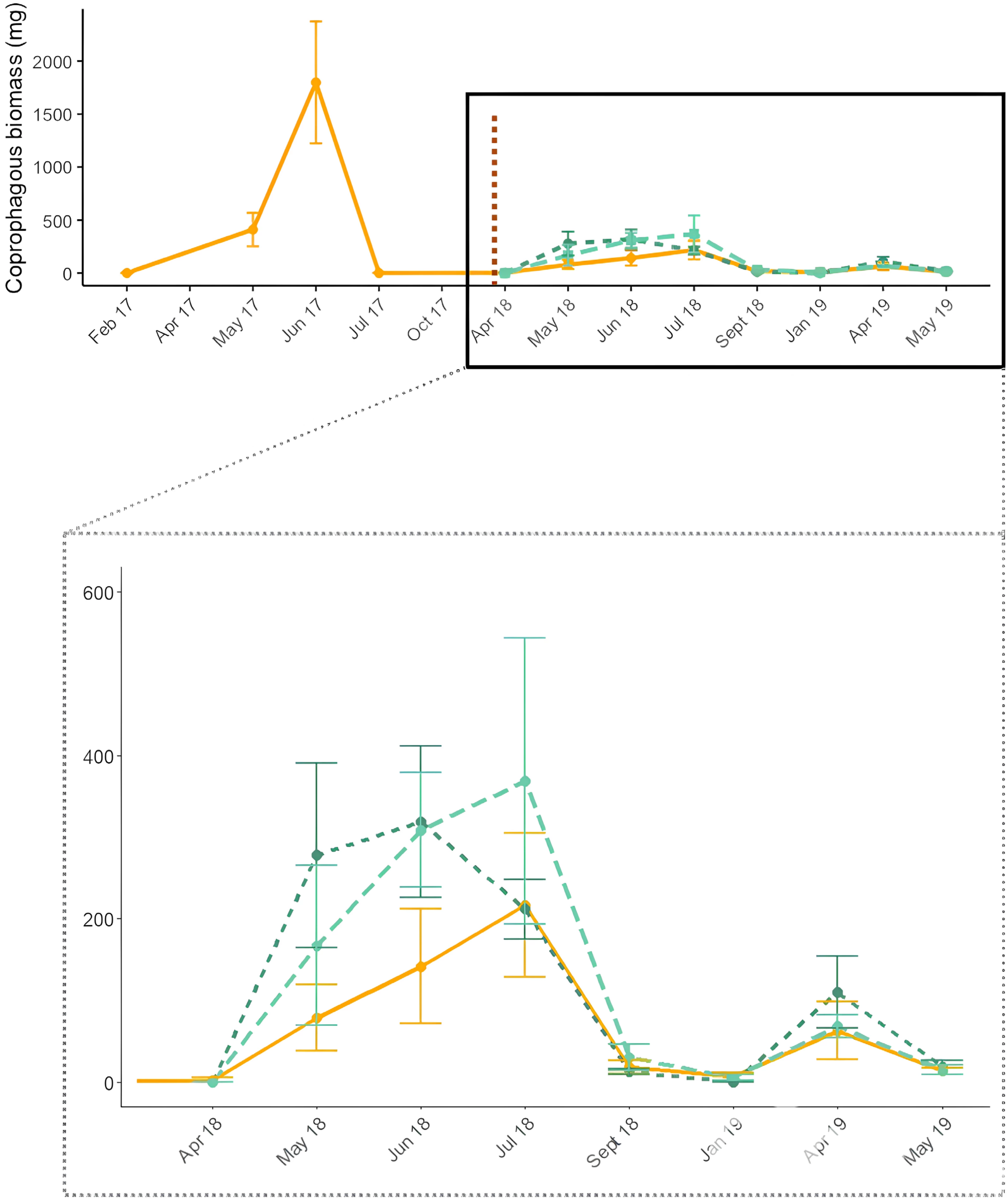

FIGURE 6 Mean ± SE of coprophagous arthropod biomass per month. Zoom in is shown for the months after dung application. Reference: Orange, VHDA: Dark aquamarine; HDA: Soft aquamarine. Brown dotted line indicates the dung input date.

explanation for the observed increase in epigeous arthropod biomass in 2018 might be in the increased herbaceous cover recorded that year, as suggested by previous studies (Bosco et al., 2019; Evans & Sanderson, 2017; Torma et al., 2014; Traba et al., 2022).

According to our predictions, dung application in experimental plots led to higher coprophagous biomass. This result, together with the decreasing coprophagous biomass in the reference area during 2018, could be explained by movements of coprophagous arthropods

TABLE 3 Averaged coefficients after fitting 1000 linear models to evaluate the effect of dung input on the space use of Dupont's Lark.

	Value	SD	95% CI
Intercept	1.84	0.19	[1.49; 2.22]
Year 2018	−1.00	0.13	**[−1.27; −0.76]**
Year 2019	−0.83	0.15	**[−1.12; −0.55]**
VHDA	1.21	0.19	**[0.83; 1.57]**
HDA	0.07	0.19	[−0.31; 0.42]
Year 2018: VHDA	0.43	0.13	**[0.19; 0.69]**
Year 2019: VHDA	0.14	0.15	[−0.14; 0.43]
Year 2018: HDA	0.60	0.13	**[0.36; 0.86]**
Year 2019: HDA	0.66	0.15	**[0.38; 0.95]**

Note: Average coefficient (Value), standard deviation (SD) and 95% confidence interval (95% CI) are shown. Intercept corresponds to Year 2017 and surrounding area as reference levels. Levels within categorical variables with significant effects are marked in bold.

from the reference area to experimental plots. Coprophagous arthropods are highly mobile (Simons et al., 2015) and very efficient in tracking the occurrence of dung (Roslin, 2000). Previous studies have described coprophagous beetle movements of up to 800 m (da Silva & Hernández, 2015). In our case, the minimum distance between experimental plots and the reference area was 730 m. Nevertheless, more information (e.g. at family level) about movement distances in coprophagous arthropods would be required for a better understanding of how coprophagous movements may explain these results. If the increase in coprophagous arthropods in the experimental plots is mediated by local movements of arthropods from neighbouring (i.e. reference) locations, it may suggest that such conservation intervention may not benefit the whole community and just modify the arthropod community at a local scale. Further research, including a BACI (before-after-control-impact) design, should aim to monitor arthropod changes over a larger period as well as to assess the impact of repeated dung treatments.

Sheep dung input had also a positive effect on epigeous arthropods, being Coleoptera the main group showing this effect. Most studies have already focused on the positive effects of extensive grazing and dung on Coleoptera abundance (Dennis et al., 1997; Melis et al., 2006), as many species in this taxon are dung-linked organisms. However, we have proven that the experimental dung application may also have positive effects on non-coprophagous epigeous arthropods (e.g. Lepidoptera order and Tenebrionidae family increased), in agreement with prior research (Grandchamp et al., 2005). The biomass of epigeous arthropods did not differ between the reference area and experimental plots during the winter and early spring of the second year after the dung application (Figure 4), which is likely attributed to the low temperatures (with snow cover for some days) in the study area during this period. Cold temperatures pose significant challenges for arthropods, as they rely on the ambient temperature to reference their physiological processes and have only limited ability to self-regulate their body temperature (Colinet et al., 2015). Although some arthropods can survive cold periods in the adult stage, many of them persist through these periods in other stages, such as the dormant late-stage larval, as is the case with certain beetles (Lincoln & Palm, 1941) or the diapausing egg stage, as seen in some cockroaches (Brown, 1973). As pitfall traps rely on arthropod movement, cold conditions limit their effectiveness, owing to reduced arthropods' activity, regardless of the life stage. In contrast, in May 2019, warmer temperatures led to a significant increase in epigeous arthropod biomass in the dung-treated areas, due to the activation of the life cycle and activity of the arthropods (Honek, 1997, see Figure 4), indicating a persistent effect of dung application for at least two springs following application. This persistence could be linked to the conditions created by the dung application in 2018, potentially resulting in enhanced arthropod reproduction or increased winter survival rates. The impact on coprophagous organisms was also observable during both springs following the application. Despite prior research suggesting rapid sheep dung decomposition, typically occurring within about 3 weeks (Williams & Haynes, 1995), our findings propose that coprophagous organisms were initially attracted to the dung after application. They might have remained in the area, not being drawn to other dung sources except from the baited traps during subsequent samplings. Consequently, these results indicate that, concerning epigeous and coprophagous arthropod biomass, a biennial dung application could be sufficient for the success of this measure, while also halving the costs.

4.3 | Effects of sheep dung input on insectivorous predators

We observed a decrease in the space use of the Dupont's lark, a typical insectivorous predator, during 2018 and 2019 compared to 2017, possibly linked to the species' ongoing decline in the study area and across Europe (Gómez-Catasús et al., 2018; Reverter et al., 2023). Despite this decline, dung application positively impacted the intensity of space use by the Dupont's lark in experimental plots over the 2 years of the study. This effect could be attributed to increased biomass of epigeous arthropods, which are a primary food source for the Dupont's Lark, since the Dupont's Lark mainly feeds on beetles and spiders (Zurdo et al., 2023). Our results agree with previous studies that found that dung may improve food availability by increasing arthropod abundance and biomass, thus finally increasing breeding productivity of some bird species, including those with conservation concern (Šálek et al., 2020). These findings suggest that dung application might be a feasible solution to rapidly improve food availability for the threatened Dupont's Lark and other coexisting species, at least in the medium term.

Here, we show that sheep dung may be a useful tool to increase the biomass of some groups of arthropods, especially coprophagous in the immediate term and non-coprophagous beetles in the short term, without modifying the original habitat. Despite being a 2-year experimental study, our results are consistent in the effect of dung

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on arthropod biomass and on a threatened insectivorous bird. The positive effect of dung input on Dupont's Lark space use, an insectivorous steppe bird commonly considered as an indicator of steppe habitat quality (Gómez-Catasús et al., 2019), also provides support for the positive impact of sheep dung on higher trophic levels while keeping habitat structure (otherwise, that specialist species would have disappeared).

Although this study focused on the effects of sheep dung input on vegetation structure, arthropod biomass and the space use of a threatened insectivorous bird, incorporating additional indicator species from different trophic levels would enhance our understanding of the ecological impacts. Due to limitations in species-level identification, we included only Dupont's lark as an indicator. Future research on the long-term effects of dung deposition on vegetation, arthropod communities and higher trophic levels could provide valuable insights for using this technique in conservation and habitat restoration under low grazing pressures. These studies need to be conducted with a complete BACI model, including a larger number of species from higher trophic levels (i.e. arthropods, birds). We would wish to highlight the pioneering character of our study, which may serve as a valuable reference for future research. Our aim is to inspire both conservation managers and scientists to explore the relationship between sheep-related practices and higher trophic levels, as to date, there are no documented cases of comparable initiatives aimed at the conservation of steppe birds.

The input of sheep dung must be understood as a one-off measure to increase food availability for insectivorous steppe species, but not as a solution to the maintenance of the Iberian steppes. In this sense, efforts should be made with the administrations to promote extensive grazing in steppe areas. Grazing should be considered as a basic measure not only to ensure habitat quality for maintaining a characteristic plant structure and composition (Zurdo et al., 2021) but also to provide habitat conditions for arthropods and ultimately insectivorous birds. Extensive grazing provides excrement in a natural way, constant over time and shapes the landscape. Just in those cases where extensive grazing is not possible, artificial dung inputs could be a solution to ensure food availability for insectivores.

AUTHOR CONTRIBUTIONS

Juan Traba conceived the research and provided funding; Margarita Reverter, Adrián Barrero, Daniel Bustillo-de la Rosa, Julia Gómez-Catasús, Julia Zurdo and Cristian Pérez-Granados performed the fieldwork; Margarita Reverter analysed the data; Margarita Reverter wrote the manuscript; Juan Traba and Cristian Pérez-Granados provided substantial edits; all authors contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Due to the sensitive nature of our research on an endangered species, the data collected in this study are confidential. Access to the data is restricted and will be granted only upon reasonable request and subject to approval by the relevant authorities.

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: Habitat management, Sheep grazing.

ORCID

Margarita Reverter https://orcid.org/0000-0003-0979-871X
Adrián Barrero https://orcid.org/0000-0002-2980-1202
Julia Gómez-Catasús https://orcid.org/0000-0001-8949-5318

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SUPPORTING INFORMATION

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

Supporting Information S1. Calculation of the amount of excrement to be applied.

Supporting Information S2. Dung application process.

Supporting Information S3. Sampling dates.

Supporting Information S4. Random points in treatment plots and surrounding area.

Supporting Information S5. Epigeous and coprophagous arthropod results by taxonomic groups.

Supporting Information S6. Cover percentages per year and treatment plot.

Supporting Information S7. Identified specimens by taxonomic group.

Supporting Information S8. Kernel density maps.

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