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Abstract

Given the impact of livestock on ecosystems worldwide, it is necessary to understand the effects of grazing practices on biodiversity in order to improve the sustainability of pasture management practices. In a pasture, spatio-temporal variability in livestock activity results in a heterogeneous distribution of defoliation, trampling and excreta. To date, fine-scale analyses of grazing intensity have been rare, and the geographical extent of the studies often limited. In this study, we addressed this gap by analysing the influence of contrasting intra-pasture grazing intensity on the structure and composition of dung beetle assemblages. To do this, we studied a three-level grazing intensity gradient in two distinct bioclimatic contexts, a Mediterranean steppe and the Alps, which also allowed us to determine if dung beetle responses to grazing intensity are related to bioclimatic conditions. The observed dung beetle responses showed an imprint of the bioclimatic context and the local pasture conditions, and species composition and relative abundance showed strong variations along the grazing intensity gradient in both study areas. Species assemblages from the most and least grazed parts of pastures differed strongly. By altering habitat conditions, changing dung availability and modifying competitive interactions, fine-scale heterogeneity in grazing intensity led to substantial variations in the abundance of dung beetle nesting guilds. In both study areas an increase in grazing intensity was detrimental to the largest species and the soil-digging species (which bury dung in underground nests), whereas dung-dwelling species (which reproduce inside dung pads) were favoured. We discuss the combined use of nesting guilds and body mass as potential features to generalize the application of dung beetles as indicators of grazing practices.

Keywords: Pastoralism; IndVal; Nesting guilds; Scarabaeoidea; Alps; Mediterranean

1. Introduction

Livestock grazing has been shown to be one of the main anthropogenic factors that have structured biodiversity for centuries in many regions worldwide (Alkemade et al., 2013). In European grasslands today, large wild ungulates have been largely replaced by domestic mammals (Bradshaw et al., 2003), which are now the most important grazers and one of the largest land-use sectors in rural economies. In the European Union, pastureland covers one-third of the area used for agriculture (European Commission, 2015). The extensive management of livestock supports rich biodiversity (Redecker et al., 2002) and is consequently promoted by European policy (Kerven and Behnke, 2011). However, the socioeconomic context drives polarization in livestock activities, with large areas left abandoned while practices are intensified in concentrated locations (Mazoyer and Roudart, 1997; Steinfeld et al., 2010). These trends in grazing intensity and livestock management are likely to cause profound changes in ecosystems (Squires et al., 2018; Stoate et al., 2009) and may have negative effects on biodiversity. The abandonment of the traditional practice of extensive grazing on rangelands reduces landscape heterogeneity, which leads to a decline in species diversity, specifically for specialist species of open habitats (García-Tejero et al., 2013; Hodgson et al., 2005; Sirami et al., 2010; Wenzel et al., 2006). Additionally, increasing livestock stocking rates may reduce species diversity (e.g. in insects, Kruess and Tscharntke, 2002; and plants, Pizzio et al., 2016), create unfavourable conditions for grassland breeding species (e.g. in birds, Paine et al., 1996) and disrupt ecosystem functioning, for example, by altering soil properties (Zhou et al., 2017).

In terrestrial ecosystems, arthropods are among the most diverse and numerous organisms, with an importance in ecosystem function inversely proportional to their small size (Wilson,

1987). A review by van Klink et al. (2015) showed that livestock effects on arthropod diversity are modulated by grazing intensity. For example, the most diverse arthropod assemblages seem to be found in heterogeneous pastures created by intermediate grazing intensity. Most of the reported results concerned predators (e.g. spiders and ground beetles) and phytophagous insects (e.g. butterflies and grasshoppers) directly affected by grazing mammals through the modification of the physical habitat (vegetation structure and cover) and plant food resources (diversity and abundance of consumed plant species) (van Klink et al., 2015). In addition to changing the structure and composition of vegetation, herbivorous mammals provide faeces (dung pads) used by many organisms for food or reproduction (Hanski and Cambefort, 1991). Of these organisms, dung beetles (Coleoptera: Scarabaeinae, Aphodiinae, Geotrupinae) are an important group involved in the key ecosystem processes of dung removal and burial (Milotić et al., 2019; Slade et al., 2007) as well as secondary seed dispersal (Griffiths et al., 2016). Without such recycling, pastures become covered by patches of grass with lower digestibility and nutritive value, rapidly becoming unsuitable for grazing (Gittings et al., 1994). To exploit ephemeral and patchily dispersed dung pads, dung beetle assemblages display a diversity of feeding and breeding strategies, reducing competition between co-occurring species (Hanski and Cambefort, 1991). In this way, dung beetles can be classified into two types of nesting guilds, based on the main strategy used by a species to exploit dung resources (Jay-Robert et al., 2008a): dung-dwellers, which develop entirely inside the dung, or soil-diggers, which relocate dung fragments in the soil for feeding and breeding. These guilds are a useful way to understand the processes by which dung beetles respond to land-use management gradients (Campos and Hernández, 2015; Jankielsohn et al., 2001; Numa et al., 2012; Tonelli et al., 2019).

89 Compared to herbivorous and predator arthropods, few studies have addressed the effects
90 of grazing intensity on dung beetle assemblages in temperate regions (van Klink et al., 2015),
91 although dung beetles are known to be good indicators of changes in environmental
92 conditions and of various anthropogenic pressures (Audino et al., 2014; Bicknell et al., 2014;
93 McGeoch et al., 2002; Spector, 2006). In Western Europe, these insects are closely linked to
94 domestic ungulates in open landscapes (Buse et al., 2015; Jay-Robert et al., 2008b; Lobo et
95 al., 2006; Macagno and Palestrini, 2009). The preference of some species for shrubby and
96 woody habitats can allow them to be used as indicators of changes in landscape structure
97 due to grazing abandonment (Tonelli et al., 2019; Verdú et al., 2011). The studies conducted
98 by Tonelli et al. (2019, 2018) in Italian pastures highlighted the negative effects of grazing
99 abandonment on dung beetles, reducing alpha diversity, evenness and dung beetle biomass,
100 as a result of insufficient dung inputs to sustain diverse assemblages. Equally, an increase in
101 intensive farming has also been shown to be detrimental to dung beetle diversity, mainly
102 due to habitat deterioration (soil trampling) from high grazing intensity (Hutton and Giller,
103 2003; Negro et al., 2011). These studies used a research approach that compared distinct
104 pastures with different stocking rates or grazing management methods. However, distinct
105 pastures may differ by more properties than stocking rate (e.g. the possible presence of wild
106 ungulates in abandoned pastures, differences in vegetation structure, use of anthelmintic
107 drugs), which makes the effects of grazing mammals per se difficult to assess. Within a
108 pasture, spatio-temporal variability in livestock activity (e.g. foraging, resting areas), which
109 depends on the type of livestock management employed, results in a spatially irregular
110 distribution of defoliation, trampling and nutrient input (from dung and urine production).
111 One might expect that the heterogeneous availability of dung and varying perturbation
112 intensity within a pasture may affect the structure and composition of dung beetle

assemblages. But while this intra-pasture variation in grazing intensity may be a more appropriate scale of analysis, it is rarely considered (however, see Chillo et al., 2017; Jerrentrup et al., 2014). Likewise, the potential use of dung beetles as indicators of local grazing practices at this fine scale of analysis has not been assessed.

In this study, we investigated for the first time the effects of contrasting intra-pasture grazing intensity on dung beetle assemblages, addressing the following questions: (i) How does grazing intensity affect the composition and structure (richness, evenness) of dung beetle assemblages at this scale? (ii) How does grazing intensity affect the abundance of the two nesting guilds, i.e. dung-dwelling and soil-digging species? (iii) Can we define indicator species for the impact of local grazing practices?

To explore these questions, we used a three-level grazing intensity gradient within extensively managed pastures with grazing practices that were as similar as possible. To our knowledge, very few previous studies have compared the effects of grazing on arthropod communities in distinct bioclimatic regions (Báldi et al., 2013; Batáry et al., 2010, 2007; Kőrösi et al., 2012; and one on dung beetles in a tropical context, Barragán et al., 2014) so we also compared two very distinct bioclimatic areas in France: a Mediterranean semi-arid lowland steppe, and mountain pastures (2000 m a.s.l.) in the Western Alps. These two areas support different dung beetle communities: one typical of Mediterranean dry steppe grasslands (Tatin et al., 2014) and one adapted to the high-altitude climate of the Alps (Lumaret and Stiernet, 1991). By comparing the dung beetle assemblage/grazing intensity relationship between the two areas, we wanted to determine if the effects of grazing depend on local conditions and species identity or if they are similar across ecological

contexts. We also expected that investigating contrasting contexts would improve the ability of using dung beetles as indicators for grazing intensity.

2. Material & methods

2.1. Study areas and sampling design

The study was carried out in pastures in two protected areas in France that differ markedly in terms of bioclimatic conditions: the Coussouls de Crau National Nature Reserve and the Vanoise National Park **(Figure 1)**. The Coussouls de Crau Reserve (hereafter, "the steppe") is a vast area of dry grasslands (11,000 ha) located near the Mediterranean Sea (43°33'N, 4°51'E) at an altitude of less than 50 m a.s.l. (Tatin et al., 2013). The climate is typically Mediterranean, with a dry season in summer, two periods of rainfall in spring and autumn, and winds above 50 $km \bullet h^{-1}$ more than 110 days a year (Devaux et al., 1983). In this plain, evidence of sheep grazing goes back to antiquity (Badan et al., 1995). Today, some 40,000 sheep still graze this semi-arid rangeland from the end of winter to early summer (Tatin et al., 2013). The grazing activity is organized in a patchwork of 70 contiguous pastures (grazing areas) through which a shepherd conducts his/her flock. During the night, the sheep are kept in a barn or in an outdoor fenced enclosure, depending on the flock size. The Vanoise National Park (hereafter, "the Alps") is located in the western Alps (45°14'N, 6°43'E) and has a typical alpine climate, with snowy winters and mild summers. The topography of the Alps has favoured high-altitude pastoralism (above 2000 m in elevation). Every year 61,000 sheep graze the alpine pastures of the National Park, following a transhumant cycle: herds are brought up to the alpine pastures in early summer and moved down to the valleys and plains in autumn. Shepherds conduct their flocks across the pasture during the day, and the sheep are kept in outdoor fenced enclosures at night. In both areas, grazing follows traditional

158 management practices that have been used for centuries: the livestock primarily graze on
159 the native vegetation of natural grasslands, except during the cold season when the animals
160 stay in barns.

161 In each study area we selected two distinct pastures **(Figure 1)** with a comparable long-term
162 grazing regime **(Appendix A)**. The small number of pasture replicates is due to the scarcity of
163 sites where we were sure that no antiparasitic treatment had been administered to the
164 sheep for at least three months prior to sampling (Beynon et al., 2012; Sands and Wall, 2018;
165 Verdú et al., 2018). The two pastures were located 6.2 km apart in the steppe, and 3.2 km
166 apart in the Alps; within a study area, both pastures had similar environmental conditions
167 **(Appendix A)**. One distinct sheep flock grazed each pasture during a four-month period on
168 average (March–June in the steppe and July–October in the Alps).

169 Based on detailed knowledge of local grazing practices provided by herders and shepherds,
170 in each pasture, we selected three zones characterized by different grazing intensity (GI),
171 which we defined as Low (LGI), Moderate (MGI) and High (HGI) **(Figure 1)**. In all the studied
172 pastures, certain zones were little exploited by shepherds. In the Alps, LGI zones
173 corresponded to areas that are usually difficult to access or had limited visibility, principally
174 due to steep terrain. In the steppe, there are no physical boundaries between contiguous
175 pastures, so the LGI zones were located at pasture edges, where shepherds only occasionally
176 take their flock to avoid the risk of grazing on neighbouring grazing areas. In these LGI zones,
177 we assumed that the availability of sheep droppings was low. The MGI zones were located in
178 main diurnal grazing zones, where shepherds regularly herd their flock each day to graze.
179 There, dropping distribution was temporally regular but spatially heterogeneous, depending
180 on the preferential foraging areas, which vary throughout the grazing season (depending on

forage availability). The HGI zones were located within or near the overnight site of the flock. These zones are characterized by intensive and repeated trampling and a high load of droppings. As each pasture contained only one overnight site (i.e. one HGI zone available to sample), it was not possible to replicate the different grazing conditions within a pasture. The mean distances between the different GI zones are shown in **Appendix B (Tables B.1, B.2)**.

In all the pastures, both in the steppe and the Alps, the vegetation was herbaceous and homogeneous across the different GI zones; isolated shrubs were found only in the least grazed zones of pastures. To validate our a priori characterization of the different GI zones, we measured the maximum height of herbaceous vegetation and the amount of sheep droppings in the representative plots where dung beetles were sampled (the protocol is detailed in **Appendix C**). We assumed that these descriptors (height of herbaceous vegetation and quantity of droppings) were good surrogates of grazing intensity levels between the different GI zones (Noy-Meir et al., 1989; Rotem, 2016; Xu et al., 2014). Moreover, they were relevant to the purpose of our study: (i) dropping availability is a key factor determining the coexistence of dung beetle species at a fine spatial scale (Finn and Giller, 2000; Horgan, 2005) and (ii) herbaceous height depends on the intensity of herbivory and on the severity of disturbance induced by sheep herds. The results showed that the maximum height of herbaceous vegetation significantly decreases while the amount of sheep droppings significantly increases in line with higher grazing intensity **(Appendix C; Figures C.1, C.2; Table C.1)**.

2.2. Dung beetle sampling

Within each LGI, MGI and HGI zone in each pasture we selected one sampling plot where dung beetles were collected using five pitfall traps (type CSR, described by Veiga et al., 1989) **(Figure 1)**. In both study areas, HGI zones had a small surface area (less than 5000 m^2). Therefore, in order to sample as homogeneous a habitat as possible in terms of grazing pressure, we placed the CSR traps 10 m apart in accordance with the standard design used in temperate contexts (Frank et al., 2017; Jay-Robert et al., 2008a, 2008b; Lobo et al., 2006; Lobo et al., 1998). The pitfall traps consisted of plastic basins (Ø 20 cm, depth 15 cm) buried to the rim in the soil, filled with water and a few drops of neutral soap, and covered with a grid, on top of which we placed 300 g of fresh sheep droppings. The traps were left open for 72 hours on sunny days during the time when dung beetle species richness and abundance is highest in the French Mediterranean (Jay-Robert et al., 2008a) and the Alps (Jay-Robert et al., 2008b): the sampling was conducted from 23 to 26 April 2018 in the steppe and from 28 July to 4 August 2017 in the Alps. Overall, 60 pitfall traps were set up (5 per level of grazing intensity × 3 GI levels per pasture × 2 pastures × 2 areas). The 15 traps used in each pasture were assumed to allow a close to exhaustive representation of the composition of local species pools (Lobo et al., 1998). All captured individuals were identified to species level using the taxonomic key provided by Paulian and Baraud (1982) and the nomenclature provided by Löbl and Löbl (2016).

2.3. Sampling completeness

Since the number of species captured in a given trap is expected to be sensitive to the number of individuals sampled (Chao et al., 2005), we calculated two estimators of asymptotic species richness based on species-incidence data, in order to test the completeness of our assemblage samples. We calculated Chao2 (Chao, 1987), which is

considered a robust estimator of minimum richness, and ICE based on estimated sampling coverage, i.e. the proportion of assemblage richness represented by the species in a set of replicated incidence samples (Lee and Chao, 1994). We used improved versions (iChao2 and ICE-1) of these indices as these increase accuracy when the heterogeneity of species abundance is relatively high (this was the case with our dataset) (Chiu et al., 2014; Lee and Chao, 1994). We used the SpadeR software (Chao et al., 2015) to compute these two species richness estimators.

2.4. Patterns in species assemblage composition

We analysed the assemblage-level responses using a Multivariate ANOVA based on a Redundancy Analysis (RDA) (Legendre and Legendre, 2012) calculated on species abundance matrices from the steppe and the Alps separately, using pitfall traps as sampling units. Redundancy Analysis is a constrained ordination method related to principal component analysis (Legendre and Anderson, 1999; Legendre and Legendre, 2012). An RDA-based MANOVA allows testing the influence of selected factors and their interaction on multivariate response matrices (in this case, species assemblages) and representing the results in triplots as in a standard RDA. The difference in community composition between the steppe and the Alps was very large, requiring no statistical tests (only 4 common species out of 52; **Appendix D**). So in order to avoid a uselessly complicated ANOVA design that would have included problematic permutation testing procedures (Anderson and Braak, 2003), we ran the test separately for each study area. In this test, we analysed the influence of two predictors on the structure of dung beetle assemblages: (i) "*pasture identity*" (two levels), and (ii) "*grazing intensity*" (three levels: LGI, MGI or HGI). We recoded these two factors as orthogonal Helmert contrasts, enabling us to test the predictors and their

interaction (Borcard et al., 2018) and reflecting our crossed sampling design within each study area (levels of grazing intensity crossed with the two pastures in each study area; **Figure 1**). Before applying the RDA-based MANOVA, we Hellinger-transformed the abundance of species to reduce the effect of extreme values and minimize the effect of double absences in the species matrices (Legendre and Gallagher, 2001). We tested the assumption of homogeneity of group dispersions (variance–covariance matrices) for the two factors with Anderson's (2006) permutation test. The significance of "*pasture identity*" and "*grazing intensity*", as well as their interaction, was assessed with pseudo-*F* permutation tests. In our case, in the presence of only two replicates for the "*pasture identity*" factor, the application of a crossed design and the consequent definition of an interaction term was a technical choice that allowed us to verify, through the interaction test, whether the effect of grazing intensity was the same in the two pastures. Since the interaction was significant, the effect of grazing intensity had to be assessed separately in each pasture. Consequently, separate one-way RDA-based MANOVAs were performed on each pasture, with "*grazing intensity*" as an explanatory factor, and R-squared values were calculated to show the percentage of variance explained. We used the R package "vegan" (Oksanen et al., 2018) (R Core Team, 2019) to test multivariate homogeneity of variance (using the *betadisper* function) and fit the RDA-based MANOVAs (using the *rda* and *anova* functions).

2.5. Number of individuals, rarefied species richness, Pielou's evenness and nesting guilds

For each pitfall trap, we measured (i) the number of captured individuals, (ii) the rarefied species richness based on the minimum number of dung beetles sampled in a trap (i.e. 15 in the steppe and 94 in the Alps), allowing us to minimize density effects (Gotelli and Colwell,

2010), and (iii) Pielou's evenness (1966). For the calculation of rarefied species richness, we removed one trap that captured only five individuals to avoid standardizing species richness from an insufficient number of individuals. However, we retained this trap to estimate variation in the other response variables studied, since removing or keeping it had no effect on models parameters. We also recorded the number of individuals belonging to the two nesting guilds, dung-dwellers and soil-diggers. Dung-dwellers develop entirely inside the dung, which they use as both a food and nesting resource (Hanski and Cambefort, 1991). Several dung-dwelling species may also lay eggs at the dung–soil interface, enabling larvae to move into the top layer of soil depending on the environmental conditions (Gittings and Giller, 1997; Landin, 1961; Lumaret and Kirk, 1991). Soil-diggers relocate dung fragments and pack them into the soil for feeding and breeding purposes. Underground nests can either be located directly beneath a dung pad or at some distance from it, as the dung can be extracted and the dung balls rolled to another location (Hanski and Cambefort, 1991). The larvae develop in a dung brood ball, or brood mass, which is packed in a chamber or at the end of a tunnel, depending on the species. In European dung beetles, small and medium-sized soil-diggers usually nest at a depth between 3 and 15 cm, while the largest species can dig nests deeper than 30 cm (Klemperer, 1979; Lumaret, 1983).

We assessed the effect of grazing intensity on the five response variables (number of captured individuals, rarefied species richness, Pielou's evenness, number of dung-dwellers and number of soil-diggers) using regressions, with pitfall traps as sampling units. Our sampling design featured two nested levels: two studied areas (steppe and Alps), each of which had two pastures **(Figure 1)**. As mentioned above, the three levels of grazing intensity (LGI, MGI and HGI) were crossed with the pasture identity. Because our aim was to compare the response of dung beetle communities to grazing between the two study areas and the

296 difference in the community composition between these areas was evident, the models
297 were fitted separately in each study area (as was done for the RDA-based MANOVAs). We
298 thus removed the highest level of the hierarchical structure (i.e. the study area). In each
299 model, we tested the effects of "*grazing intensity*" (fixed factor with three levels: LGI, MGI,
300 HGI) on the five response variables described above. One can consider the "*pasture identity*"
301 as a random factor, as the pastures we sampled were chosen from a large number of
302 pastures in each study area. However, the insufficient number of independent pastures in
303 each study area (n = 2) prevented us from applying mixed models with this factor as a
304 random effect, as mixed model estimation requires a reasonable number of random-effects
305 levels. Gelman and Hill (2007) argue that when the number of groups is small (less than five),
306 there is not enough information to accurately estimate group-level variation. As a result,
307 multilevel models in this context typically gain little relative to standard models. Thus, we
308 used standard linear and generalized linear models, considering the "*pasture identity*" as a
309 fixed effect. In the Results section, we focus on the effects of the "*grazing intensity factor*" –
310 the results for the "*pasture identity*" factor are presented in **Appendix E**. Generalized linear
311 models allow the use of non-Gaussian error distribution, which was especially useful for
312 count data in our case (i.e. number of individuals, dung-dwellers and soil-diggers). We
313 systematically corrected for Poisson overdispersion using a negative binomial family
314 (Gardner et al., 1995). We used the R packages "stats" (using the *lm* and *glm* functions) and
315 "MASS" (Venables and Ripley, 2002) (using the *glm.nb* function) to fit the models.

316 *2.6. Indicator species analysis*

317 To identify indicator species for grazing intensity, we calculated the IndVal index (Dufrêne
318 and Legendre, 1997). The IndVal combines the degree of specificity (highest when the

species is present in a given habitat type but not elsewhere) and fidelity (highest when the species is present in all sites of a given habitat type). The closer the IndVal value is to 1, the higher the specificity and/or fidelity of a species to a given level or pair of levels of grazing intensity. We calculated this index on non-transformed species abundance matrices, using pitfall traps as sampling units, to individual levels of grazing intensity and their combinations (i.e. LGI/MGI and MGI/HGI) based on the approach by De Cáceres and Legendre (2009). We ran the analysis separately for each studied area (steppe and Alps), and assessed the statistical significance of the IndVal values by means of a permutation test with a 5% rejection threshold (Dufrêne and Legendre, 1997). We associated each selected indicator species with its species-specific nesting guild and mean body mass. The latter was measured by randomly selecting between 4 and 10 individuals per species (depending on the number available) and weighing them after drying them at 70 °C for 24 h. We used this information to improve the ecological interpretation of the results and make it more accessible for non-specialists of dung beetles. We used the R package "indicspecies" (using the *multipatt* function) to find indicator species for different grazing intensity levels (De Cáceres and Legendre, 2009).

3. Results

3.1. Dung beetle inventories

We collected a total of 11,733 dung beetles belonging to 52 species (see **Table 1** and **Appendix D** for the complete list of the sampled species). While species richness was higher in the steppe, the number of individual beetles captured was seven times higher in the Alps **(Table 1)**. The species composition in the two study areas was very different, with only four

342 species in common (*Aphodius cardinalis, Calamosternus granarius, Colobopterus erraticus*
343 and *Otophorus haemorrhoidalis*; **Appendix D**). The five most abundant species were *C.*
344 *granarius*, *C. erraticus*, *Euorodalus paracoenosus*, *Onthophagus ruficapillus* and *O. vacca* in
345 the steppe; and *Amidorus obscurus*, *Euheptaulacus carinatus*, *Oromus alpinus*, *Onthophagus*
346 *fracticornis* and *Parammoecius corvinus* in the Alps **(Appendix D)**. In the Alps, we collected
347 four large species of the Geotrupinae subfamily (*Geotrupes stercorarius, Anoplotrupes*
348 *stercorosus, Trypocopris vernalis* and *T. alpinus*), which are absent in the steppe ecosystem.
349 The iChao 2 and ICE-1 species richness values show that our sampling was relatively
350 exhaustive, representing 75–98% of the estimated species richness in the study area
351 considered **(Table 1)**.

352 *3.2. Patterns in species assemblage composition*

353 For all the subsequent analyses, we removed 9 singleton species, retaining 43 species. In
354 both study areas, the RDA-based MANOVAs showed a significant effect on dung beetle
355 species assemblages of "*pasture identity*" (steppe, $F_{1, 28} = 7.67$, $p = 0.001$; Alps, $F_{1, 28} = 60.75$,
356 $p = 0.001$) and of "*grazing intensity*" (steppe, $F_{2, 27} = 22.10$, $p = 0.001$; Alps, $F_{2, 27} = 42.85$, $p =$
357 0.001). The interaction between these two factors was also significant in the steppe ($F_{2, 27} =$
358 4.46, $p = 0.001$) and the Alps ($F_{2, 27} = 29.93$, $p = 0.001$), meaning that the effect of grazing
359 intensity on species assemblages differed significantly according to the pasture considered.
360 Thus, we ran RDAs constrained by the grazing intensity factor and plotted the results
361 (triplots) separately for each pasture in each study area. In the steppe, grazing intensity
362 explained 74.8% and 58.7% of the total variation in species assemblages respectively in
363 pastures A and B **(Figure 2)**. Most of the variation was explained by the first axis of each
364 RDA, which gathered 78–93% of the variation explained by the constraining factor. In both

steppe pastures, the first axis of the triplots clearly differentiated the two endpoints of the grazing intensity gradient, showing the HGI plots on the left, and the MGI and LGI plots on the right of the ordination planes. In steppe pasture A, species assemblages of the HGI plot were more distinct from the other plots than in pasture B. Moreover, the MGI and LGI plots were not particularly contrasted along the second axis, which explained a low percentage of variation (5%). In pasture B, the second axis explained a larger percentage of variation (13%) and showed contrast between the MGI and LGI plots.

In the Alps, grazing intensity explained 89.9% and 82.9% of the total variation in species assemblages respectively in pastures C and D **(Figure 3)**. As in the steppe, most of the variation was explained by the first RDA axis (70–80%), which clearly differentiated the LGI plots on the left and HGI plots on the right of the ordination planes. The second axis of each RDA triplot differentiated the MGI plots from the other grazing intensity levels.

A comparative analysis of the results indicated that (i) the grazing intensity gradient structured the dung beetle species assemblages in all the studied pastures; (ii) in each studied area, the level of differentiation between assemblages along the gradient was dependent on the pasture considered; and (iii) species assemblages showed more contrast due to grazing intensity in the Alps than in the steppe.

3.3. Number of individuals, rarefied species richness and Pielou's evenness according to grazing intensity

When the "*pasture identity*" factor was held constant, "*grazing intensity*" had differing effects on the response variables reflecting dung beetle community structure. In the steppe, the number of captured individuals and the rarefied species richness did not show any significant response to grazing intensity **(Figure 4A)**. Pielou's evenness was higher in HGI

plots compared to LGI plots, but values of MGI plots were no different from the other two levels of grazing intensity. In the Alps, the number of captured individuals was higher in MGI and HGI plots and lower in LGI plots **(Figure 4B)**. The rarefied species richness was higher in LGI plots than in MGI and HGI plots. An inverse relationship was observed for Pielou's evenness, which progressively and significantly increased with grazing intensity.

When the "*grazing intensity*" factor was held constant, there were no significant differences in the number of captured individuals, rarefied species richness or Pielou's evenness between the two sampled pastures in the steppe **(Appendix E, Figure E.1)**. In the Alps, there were significantly more individuals sampled in pasture C, whereas the rarefied species richness was higher in pasture D **(Appendix E, Figure E.1)**.

3.4. Nesting guild abundance according to grazing intensity

When the "*pasture identity*" factor was held constant, "*grazing intensity*" had similar effects on the nesting guild abundance in the two study areas. The results of the models showed that, in both study areas, the abundance of dung-dwellers significantly increased between LGI and HGI plots **(Figure 5)**. The MGI plots occupied an intermediate position between the two other levels in the steppe, but MGI and HGI plots did not differ from each other in the Alps. The abundance of soil-diggers significantly decreased between LGI and HGI plots in the Alps, whereas in the steppe, no significant variation was observed **(Figure 5)**. However, because the p value between MGI and HGI plots was close to 0.05 (0.0573), we cannot completely exclude a possible effect of grazing, and thus a tendency towards a decrease in soil-diggers between moderate and high grazing intensity zones (Amrhein, Greenland, & McShane, 2019).

When the *"grazing identity"* factor was held constant, there were more dung-dwellers caught in pasture B than in pasture A in the steppe, while there was no difference in the number of soil-diggers **(Appendix E, Figure E.2)**. In the Alps, there were significantly more dung-dwellers and soil-diggers captured in pasture C than in pasture D **(Appendix E, Figure E.2)**. This pattern can be explained by the greater overall abundance observed in pasture C **(Appendix E, Figure E.1)**.

3.5. Indicator species

In the steppe, half of the species collected (excluding singletons) were retained as indicators of grazing intensity **(Table 2)**. Six species were indicators for individual grazing intensity levels, and six others for combined levels. *Copris hispanus hispanus*, by far the largest beetle of the 12 indicator species identified, was the only indicator species for LGI plots. We found that the body mass of indicator species belonging to the soil-digger guild decreased between LGI/MGI plots and MGI/HGI plots. Including both nesting guilds, indicator species for the LGI/MGI combination covered a relatively large range of body mass values, from 2.8 ± 0.8 g to 67.7 ± 13 g. Only soil-diggers were associated with MGI plots and the MGI/HGI combination, while indicators for HGI plots were mostly dung-dwellers.

Of the 22 species collected in the Alps (excluding singletons), only 4 (18%) were selected as indicators of grazing intensity **(Table 2)**. In this area, we only found species indicators for LGI plots and the combination MGI/HGI plots. Two large soil-digging species (*Geotrupes stercorarius* and *Trypocopris vernalis*) were associated with low grazing intensity, while the only species associated with MGI/HGI plots was a small dung-dweller (*Oromus alpinus*), 30 to 50 times lighter. One species, *Otophorus haemorrhoidalis*, collected in both study areas, was

found to be an indicator for LGI plots only in the Alps. The position of some of the indicator species found is shown on the ordination planes of the RDAs in **Figures 2** and **3**.

Discussion

Overall, our results show that the intra-pasture variation in grazing intensity exerted by domestic ungulates strongly structured dung beetle species assemblages. Beyond the effects of the bioclimatic context and the local pasture conditions, the dung beetle communities showed strong response patterns to variation in grazing intensity in the two study areas. Whereas species assemblages were more contrasted along the grazing intensity gradient in the alpine pastures, the observed differences reflected substantial variation in nesting guild abundance in both areas. This result is all the more significant since less than 10% of the species were common between the steppe and the Alps. Furthermore, taking nesting guild into account offers deeper insights about the effects of grazing on dung beetle assemblages.

4.1. Sampling effectiveness

The iChao2 and ICE-1 estimates showed that by sampling during the peak of dung beetle activity we were able to obtain a quite exhaustive representation of local species assemblages inhabiting the studied pastures. According to Lobo et al. (2006), as the emergence of dung beetles during their maximum activity period depends on the habitat conditions of the previous year at the same period, we assumed that targeting these activity peaks would be relevant for investigating the effects of various grazing conditions. In the steppe, we collected 64% of the total dung beetle species richness known to occur in the area, based on inventories conducted in the Coussouls de Crau National Nature Reserve over

five years of successive sampling in eight different pastures during spring and autumn (Tatin et al., 2014 and unpublished results). In the Alps, we recorded 70% of the total species richness previously inventoried in the total area of the Vanoise National Park based on intensive sampling carried out across all seasons (Lumaret and Stiernet, 1991). Previous large surveys conducted in France both in Mediterranean ecosystems (Jay-Robert et al., 2008a) and in the western Alps (Jay-Robert et al., 2008b) have shown that the seasonal activity of Scarabaeinae species is mainly restricted to spring/early summer (depending on elevation) and that only Aphodiinae species were temporally segregated, with an activity period from early spring to late autumn (and even winter at the lowest elevations). Consequently, sampling in spring/summer was effective for studying diverse assemblages composed of a mixture of coexisting dung-dweller and soil-digger species.

4.2. Intra-pasture variation in grazing intensity shapes the structure and composition of dung beetle assemblages

In central Italy, Tonelli et al. (2017) previously found significant contrasts in the composition of dung beetle assemblages between pastures subjected to low and moderate grazing intensity. Our results reveal that such differences also exist within pastures. This corroborates studies showing that differences in the composition and structure of terrestrial arthropod assemblages often reflect fine-scale habitat heterogeneity (Gonçalves-Souza et al., 2015; Weiss et al., 2016). In our case, as the vegetation in the different GI zones was similar (grasslands without shrubs, see “Material & methods”), we suggest that fine-scale variation in habitat conditions in terms of droppings availability and disturbance intensity (especially trampling) might be the main cause of the observed changes. The difference in species composition between pastures might explain the significant interaction between

pasture identity and grazing intensity. However, the similar patterns showed by the multivariate analyses between the steppe and the Alps suggest that the grazing intensity gradient had a similar effect whatever the bioclimatic context. In each pasture, the multivariate analyses show that species assemblages were significantly different across the three levels of the grazing intensity gradient. In addition, the RDA-based MANOVAs show that the sampled zones that were spatially closest **(Appendix B)** were clearly distinguished from one another. Dung beetles are known to have a high dispersal capacity, necessary to find ephemeral and patchily distributed dung pads (Roslin and Viljanen, 2011). They are able to forage over hundreds of metres (Roslin, 2000), across distances exceeding those separating our sampling plots. However, despite the capacity of the observed species to colonize the spatially closest sampled zones, thus possibly inducing positive spatial autocorrelation between them, the observed patterns show a greater imprint of the local grazing conditions.

The increased droppings availability in moderately and highly grazed zones of pastures allowed more individuals to coexist in the Alps. This corroborates the results of Lumaret et al. (1992) showing that the abundance and biomass of dung beetles strongly depend on the quantity of trophic resources. If ungulate grazing is considered a disturbance process (Hobbs, 2006), one might expect that an increase in grazing intensity would promote the coexistence of a few well-adapted and numerically dominant species, with the other species remaining in low numbers (Grime, 1973), resulting in decreasing evenness. Surprisingly, we observed that the evenness of species assemblages significantly increased along the grazing intensity gradient in both study areas. This result may be explained by a level of disturbance resulting from grazing that was still not strong enough, even in the most intensively grazed zones sampled. However, resource scarcity favoured the dominance of a lower number of species

501 in the least intensively grazed zones, which is likely to explain the decrease in species
502 evenness. Theoretically, the most competitive and/or efficient species are more suited for
503 exploiting limited resources (Connell, 1978). In our surveys, two dung beetles belonging to
504 the *Onthophagus* genus were particularly abundant in the least grazed habitats: *O. vacca*
505 accounted for almost 70% of the abundance in LGI plots in the steppe, and *O. fracticornis*
506 represented half of the abundance in LGI plots in the Alps **(Appendix D)**. In central Italy,
507 Tonelli et al. (2018) obtained similar results, finding that *Onthophagus* were among the most
508 common species in an abandoned pasture. Taken together, these findings suggest that
509 *Onthophagus* species are efficient foragers, allowing them to maintain their population in
510 habitats where dung is relatively scarce, such as in the least grazed zones of pastures.

511 Although both study areas shared many similar results, the species assemblages observed in
512 the Alps were more differentiated along the grazing intensity gradient than in the steppe,
513 reflecting differences in livestock management. While herd sizes were similar in both study
514 areas, sheep density was more than twice as high in the Alps as in the steppe (11.8 vs 4.7
515 sheep/ha; **Appendix A**). As higher livestock density results in higher droppings input and soil
516 trampling, this is likely to increase habitat heterogeneity within the pasture, leading to
517 contrasting habitat conditions between moderate and low grazing zones, and thus increasing
518 the differences in dung beetle assemblages. Hence, the lower livestock density in the steppe
519 is likely to explain that dung beetle assemblages inhabiting low and moderate grazing zones
520 were more similar to each other than they were to assemblages in high grazing zones.

521 Previous studies have reported a decrease in observed species richness with an increase in
522 grazing intensity for different arthropod taxa such as grasshoppers, butterflies,
523 hymenopterans and moths, mainly due to homogenization of vegetation structure and

524 diversity, but also to changes in trophic interactions (Enkhtur et al., 2017; Kruess and
525 Tscharntke, 2002). On this question, we found contrasting results between the two study
526 areas. While in the Alps rarefied species richness decreased with an increase in grazing
527 intensity in moderate and high grazing zones of pastures, in the steppe, the turnover in
528 species composition along the grazing intensity gradient did not lead to significant changes
529 in rarefied species richness. Several processes may explain the differences we observed
530 between the two study areas. Of these, specific historical anthropogenic processes (i.e. the
531 history of local grazing practices) and abiotic constraints (e.g. climate) are very likely to
532 separately drive the establishment of current dung beetle species assemblages and the
533 interspecific interactions that take place in the steppe and the Alps. In the Cévennes
534 National Park, an intermediate location between the steppe and the Alps (44°20'N, 3°50'E;
535 800 m a.s.l.), Jay-Robert et al. (2008c) observed higher species richness and temporal
536 turnover in the dung beetle assemblages of grazed shrubland than in those of grazed
537 grasslands, where dung resources were twice as high. In this region of low mountains, dung
538 beetle diversity was thus more limited by the homogeneous structure of the herbaceous
539 habitat than by resource availability. Considering that short vegetation covers the steppe
540 whatever the grazing intensity (Devaux et al., 1983), one may hypothesize that habitat
541 heterogeneity was too low to make a difference to the number of coexisting species
542 throughout the grazing intensity gradient.

543 *4.3. Nesting guilds reflect the effects of grazing intensity*

544 Differences in dung beetle nesting guild abundance in abandoned and moderately grazed
545 pastures have been reported in southern Europe (Tonelli et al., 2019). Our findings showed
546 that such differences also occur in response to fine-scale variation in grazing intensity within

547 pastures. The shifts observed in nesting guild abundance support the previously discussed
548 differences in the overall structure and composition of dung beetle assemblages along the
549 grazing intensity gradient. The similarity in the trends observed between the steppe and the
550 Alps indicates that the filtering effect exerted by grazing pressure selects species according
551 to particular traits, allowing them to persist at different levels of grazing intensity.

552 Dung-dwellers were significantly more abundant in zones of high and moderate grazing
553 intensity than in those of low grazing intensity, whereas the abundance of soil-diggers
554 tended to decrease when grazing intensity increased. In overgrazed habitats, vegetation is
555 permanently short. Hard trampling increases soil compactness and creates patches of bare
556 soil, leading to a warmer underground microclimate and promoting water evaporation
557 (Greenwood and McKenzie, 2001; Lu et al., 2017; Yan et al., 2018; Zhou et al., 2010).
558 Significant changes in soil moisture and physical conditions may compromise the ability of
559 some soil-digger species to dig efficiently (Dabrowski et al., 2019) or the suitability of the
560 underground habitat for their larvae (Sowig, 1996, 1995). Hutton and Giller (2003) and
561 Negro et al. (2011) also observed a decrease in the abundance of soil-diggers in overgrazed
562 and intensively managed pastures in lowland Ireland and the Italian Alps, respectively.
563 Because of their autecological requirements, dung-dwellers might be less sensitive to soil
564 properties than soil-diggers; however, the quantity of available resources is an important
565 factor driving their abundance (Lumaret et al., 1992). Their dwelling behaviour does not
566 involve food relocation, so the maintenance of local populations depends solely on the
567 presence of dung and the preservation of this resource during larval development (Gittings
568 and Giller, 1999, 1997).

569 Typically, dung pads are an ephemeral and patchily distributed resource. Several studies
570 support the hypothesis that strong competition for local resources occurs both between
571 coexisting individuals and dung beetle species (Finn and Gittings, 2003; Giller and Doube,
572 1994, 1989; Gittings and Giller, 1999). In addition, sheep droppings are a relatively scarce
573 resource for dung beetles, occurring in much smaller quantities and drying out rapidly
574 compared to cattle dung, which can gather hundreds of individuals (Finn and Gittings, 2003;
575 Lumaret, 1995; Lumaret et al., 1992). Soil-diggers are usually known to be faster at resource
576 acquisition than dung-dwellers (Hanski and Cambefort, 1991), which could explain their
577 dominance in the least grazed parts of pastures. Highly abundant at low grazing intensity,
578 the previously mentioned *Onthophagus* species are soil-diggers that build ramified tunnels
579 below droppings or dung pads. The foraging efficiency of soil-diggers allows them to rapidly
580 access and secure the few resources available, conferring an advantage in resource-scarce
581 environments. Because of their high competitiveness in resource acquisition, an increase in
582 soil-digger abundance is likely to lead to more competitive interactions (Connell, 1978) and
583 to prevent the installation of dung-dwellers. In the Alps, the largest soil-diggers we collected
584 – *Geotrupes stercorarius* and *Anoplotrupes stercorosus* (Geotrupinae) – were much more
585 abundant in low grazing zones **(Appendix D)**. Geotrupinae species are fast burrowers able to
586 build deep tunnels filled with large faecal masses in only 24 hours (Klemperer, 1979).
587 Gittings and Giller (1999) showed that, by rapidly removing dung pads from the surface of
588 the ground, Geotrupinae abundance can negatively impact the reproductive success of
589 dung-dwellers. This intense exploitative competition may be one of the factors explaining
590 the decrease of dung-dwellers we observed in the least grazed parts of pastures.

591 For arthropods, the heterogeneity in vegetation structure and abiotic conditions created by
592 a moderate level of grazing often promotes more diverse assemblages than at low and high

593 grazing levels, favouring the occurrence of species with different habitat requirements (van
594 Klink et al., 2015). Our results partially support this general finding: although species richness
595 did not peak at intermediate grazing intensity, both dung-dwellers and soil-diggers were
596 found in high abundance in moderate grazing zones of pastures. Moderate sheep grazing
597 results in a patchy distribution of droppings and heterogeneous soil conditions and
598 vegetation cover, creating a variety of habitats suitable for species with diverse nesting
599 strategies. With a moderate level of habitat disturbance, one could hypothesize that a
600 balance exists between competitive exclusion and loss of competitive dominants through
601 disturbance, these conditions favouring the coexistence of competitive species (soil-diggers)
602 and disturbance-tolerant species (dung-dwellers) (Connell, 1978; Mackey and Currie, 2001).

603 *4.4. Can dung beetles be relevant indicators of grazing intensity effects?*

604 As expected, given the strong compositional difference in dung beetle assemblages between
605 the steppe and the Alps, we found different indicator species in each study area.
606 Nevertheless, the body mass and nesting behaviour of indicator species highlighted a similar
607 trend: irrespective of species identity, the largest soil-digger indicator species were
608 associated with relatively low grazing intensity, while the indicator species for higher grazing
609 intensity were mostly either small soil-diggers or small dung-dwellers. The indicator species
610 for moderate grazing levels covered a large range of body mass values and belonged to both
611 nesting guilds. This pattern was especially well defined in the steppe since soil-diggers were
612 almost twice as diverse in the Mediterranean lowland as in the alpine highland (14 vs 8 soil-
613 digger species in the steppe and in the Alps, respectively; Jay-Robert et al., 1997).

614 Generally, the smallest dung beetle species are known to be more fecund than the largest
615 (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). Compared to soil-diggers, dung-

dwellers show higher fecundity and ovipositing rates (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Gittings and Giller, 1997). In Scarabaeinae soil-diggers, the largest species are usually less fecund, compensated by a high level of parental care. In the steppe, the largest soil-digger indicator species, *Copris hispanus hispanus* and *Gymnopleurus flagellatus flagellatus*, were indicators of low and low/moderate grazing intensity, respectively. They have a lower reproductive rate compared to the smaller soil-diggers (*Onthophagus* species; Halffter and Edmonds, 1982) that we found as indicators of higher grazing intensities. It is possible that these large soil-diggers are less able to produce a replacement clutch if repeated trampling destroys the previous one (as Simons et al. (2016) concluded about the response of various arthropods to flooding intensity). Additionally, the largest species are known to forage across larger areas than the smallest species, thus suggesting greater dispersal capacity for large dung beetles (Peck and Howden, 1984; Roslin, 2000, 2001). This may confer these beetles with a greater ability to maintain their populations in the least grazed parts of pastures where resource availability is low. Nevertheless, there are very few quantitative descriptions of dung beetle dispersal and foraging behaviour, preventing detailed hypotheses. As we did not analyse body-size patterns exactly along the grazing intensity gradient, these interpretations should be taken with caution. Further studies are needed to more accurately determine the relationship between the biology of dung beetle species and their ability to persist subject to distinct levels of grazing.

Other studies have previously identified several of our indicator species as characteristic of comparable habitat conditions in Europe. In Ireland, Hutton and Giller (2003) found that *Geotrupes stercorarius*, one of the largest soil-diggers occurring in northern temperate dung beetle communities, was significantly more abundant in extensively managed pastures (on

640 organic farms). In the French Alps, we found this species was an indicator for the least
641 grazed zones of pastures. We can hypothesize that *Geotrupes stercorarius* is able to maintain
642 its population in resource-scarce environments thanks to its foraging efficiency, avoiding the
643 most trampled habitats with high soil disturbance. In the Mediterranean region, (J.-P.
644 Lumaret & Iborra, 1996) found high numbers of *Aphodius foetidus* and *Calamosternus*
645 *granarius* inhabiting dropping accumulations where sheep rest. We corroborated this
646 observation in the steppe, where we found that these two species were indicators for the
647 most grazed zones of pastures. *Calamosternus granarius*, which is a cosmopolitan species
648 originating from the Palearctic region, ranks among the smallest of the dung-dwellers in
649 Europe and is considered a generalist feeder (Gittings and Giller, 1997). Brown (1940), Sears
650 (1978) and Ratcliffe (1991) showed that this species feeds on a variety of faeces, carrion and
651 compost material. The generalist diet of *Calamosternus granarius* is likely to allow
652 individuals to consume and to breed on the accumulated manure produced by livestock in
653 overgrazed areas.

654 Given the wide distribution of *Geotrupes stercorarius* (introduced in North America; Brown,
655 1940), *Calamosternus granarius* (introduced in North America, Australia and the Afro-
656 tropical region; de Jong et al., 2014) and *Aphodius foetidus* (widely distributed in Western
657 Europe; Lumaret, 1990), we would recommend extending their use as indicators of grazing
658 practices to other regions. However, species found to be indicators in a given area may not
659 be transposable elsewhere because of changes in species pool composition across distinct
660 bioclimatic contexts. Practically speaking, the use of a set of indicator species may thus be
661 restricted to a particular locality or region (Zettler et al., 2013), so our IndVal results are
662 likely difficult to generalize if only species identity is considered. Integrating species traits (as
663 we did with nesting guild and body mass) improves the ecological interpretation of IndVal

664 results. This suggests a way to bypass dung beetle taxonomy, which requires specialist
665 knowledge. Dung beetles collected in the field can be easily classified as dung-dwellers or
666 soil-diggers in different weight classes (or size, which is easier to measure and correlates
667 with body mass), avoiding the need for difficult species identification training. The use of
668 body size and nesting guilds as indicator measures would be an easier method for
669 conservation practitioners, improving the use of dung beetles as indicators for impacts of
670 local grazing practices. To increase the scope of our results and the usability of this method,
671 we recommend comparing findings from studies carried out in different bioclimatic contexts
672 and across a higher number of pastures.

673

674 ## Conclusion

675 Working at an intra-pasture scale and selecting sheep-grazed pastures with similar grazing
676 histories, we were able to analyse the processes by which the pressure of domestic
677 ungulates can substantially modify the composition and structure of dung beetle
678 assemblages. Our results suggest that, by altering habitat conditions, changing droppings
679 availability and modifying competitive interactions, fine-scale variation in grazing intensity
680 leads to substantial variations in nesting guild abundance. High grazing intensity is
681 detrimental to soil-diggers and the largest dung beetle species. Whereas some of these
682 species (e.g. *Gymnopleurus flagellatus flagellatus*) have historically declined in Western
683 Europe due to a progressive decrease in extensive grazing practices (Caillol, 1908; Carpaneto
684 et al., 2007; Lobo, 2001), local intensification of livestock farming may not compensate for
685 grazing abandonment on surrounding lands. Conversely, small dung-dwellers are favoured in
686 highly grazed habitats, where sheep droppings are predictable and highly available. These

687 results show that grazing intensity acts as an environmental filter on dung beetle
688 assemblages, selecting species according to particular traits. In order to better understand
689 the mechanisms by which grazing practices influence the structure of these assemblages,
690 further studies could integrate life-history trait approaches (e.g. Chillo et al., 2017).

691

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701

702 ## Appendices

703 **Appendix A.** General information for each pasture in each study area regarding: grazing
704 practices (historical and present) and environmental conditions (vegetation, soil type,
705 climate).

706 **Appendix B.** Distances between the different GI zones in each pasture and in each study
707 area.

Appendix C. Characterization of the grazing intensity gradient.

Appendix D. Abundance of dung beetle species collected in the two study areas, the steppe and the Alps.

Appendix E. Effect of "*pasture identity*" on dung beetle assemblages.

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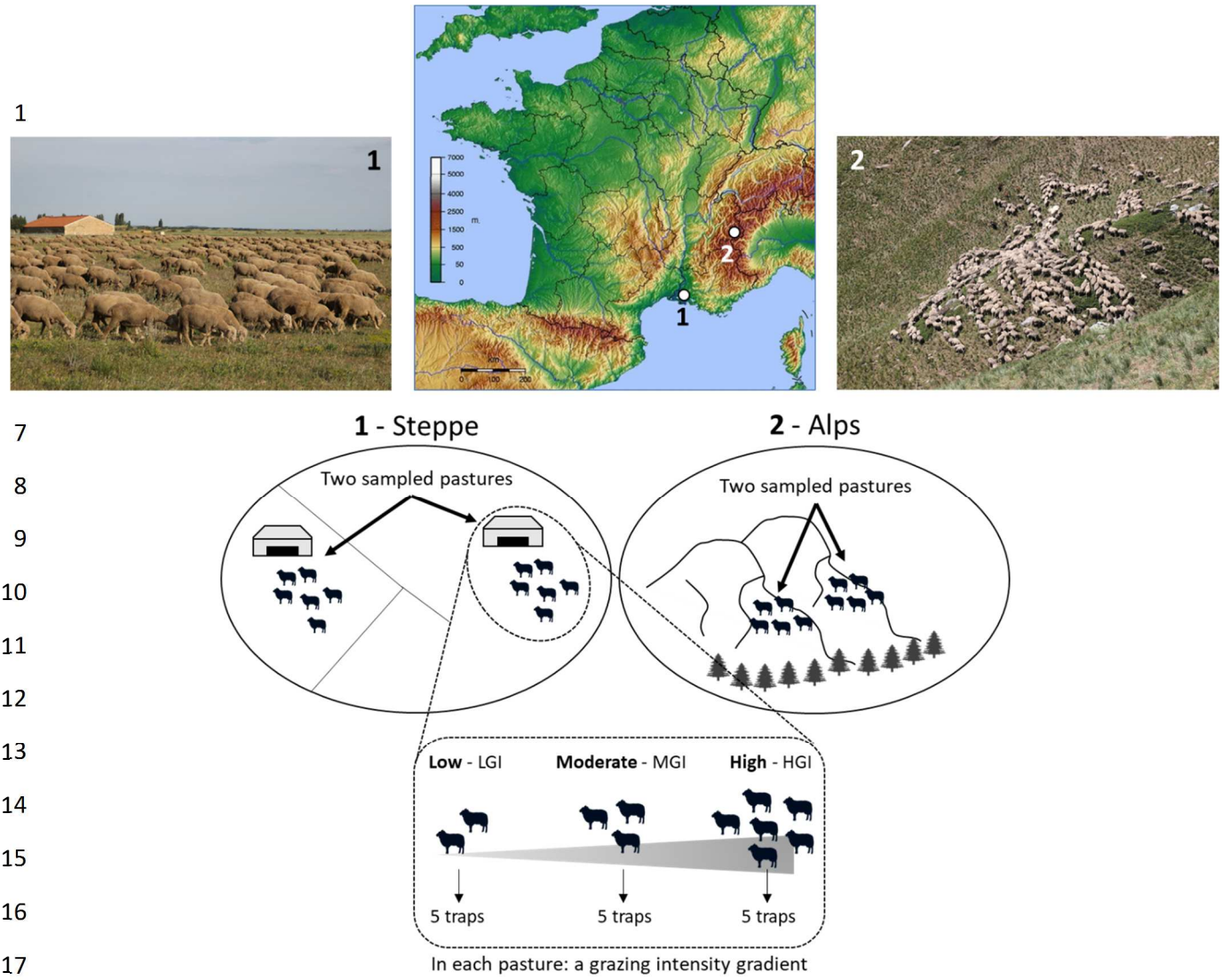

Figure 1. Location of the two study areas representing two distinct bioclimatic contexts, (1) the Coussouls de Crau National Nature Reserve (steppe) near the Mediterranean Sea, and (2) the Vanoise National Park (Alps) in the northern French Alps (map of France: https://upload.wikimedia.org/). Illustration of sheep flocks in these two areas (photographs ©William Perrin) and schematic representation of the sampling design and the grazing intensity gradient. In each study area, two distinct pastures were sampled. Within each pasture, we defined three distinct zones representing three levels of grazing intensity, ranging from low (LGI) to moderate (MGI) to high (HGI) (although we show the grazing intensity gradient for just one pasture, the same sampling design was carried out in each of the four pastures). Within each level of grazing intensity, we selected a sampling plot where dung beetles were collected with five pitfall traps.

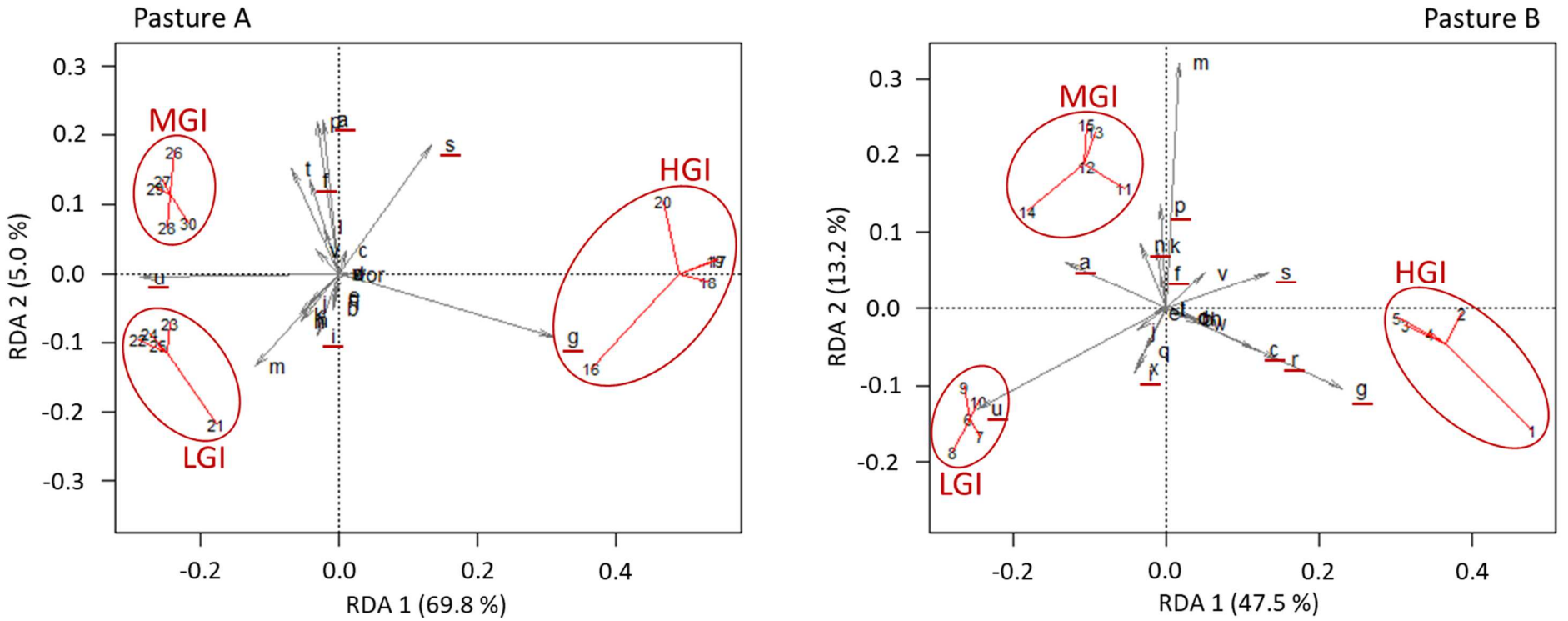

Figure 2. Triplots of RDA-based MANOVAs for the two pastures (A and B) sampled in the steppe area. Numbers represent the traps, whose "wa" scores are related to the centroids of the grazing intensity factor (three levels: Low = LGI, Moderate = MGI and High = HGI) by means of straight lines, in scaling 1. Ellipses represent the three distinct grazing intensity levels in each pasture. Letters represent the species. The percentage of variation explained by the RDAs is shown for each axis. Underlined letters correspond to indicator species found in the IndVal analysis **(Table 2)**: *Acrossus luridus* (a); *Aphodius foetidus* (c), *Caccobius schreberi* (f), *Calamosternus granarius* (g), *Copris hispanus hispanus* (i), *Gymnopleurus flagellatus flagellatus* (n), *Onthophagus furcatus* (p), *Onthophagus opacicollis* (r), *Onthophagus ruficapillus* (s), *Onthophagus vacca* (u). See **Appendix D** for letters identifying the other species on the triplots.

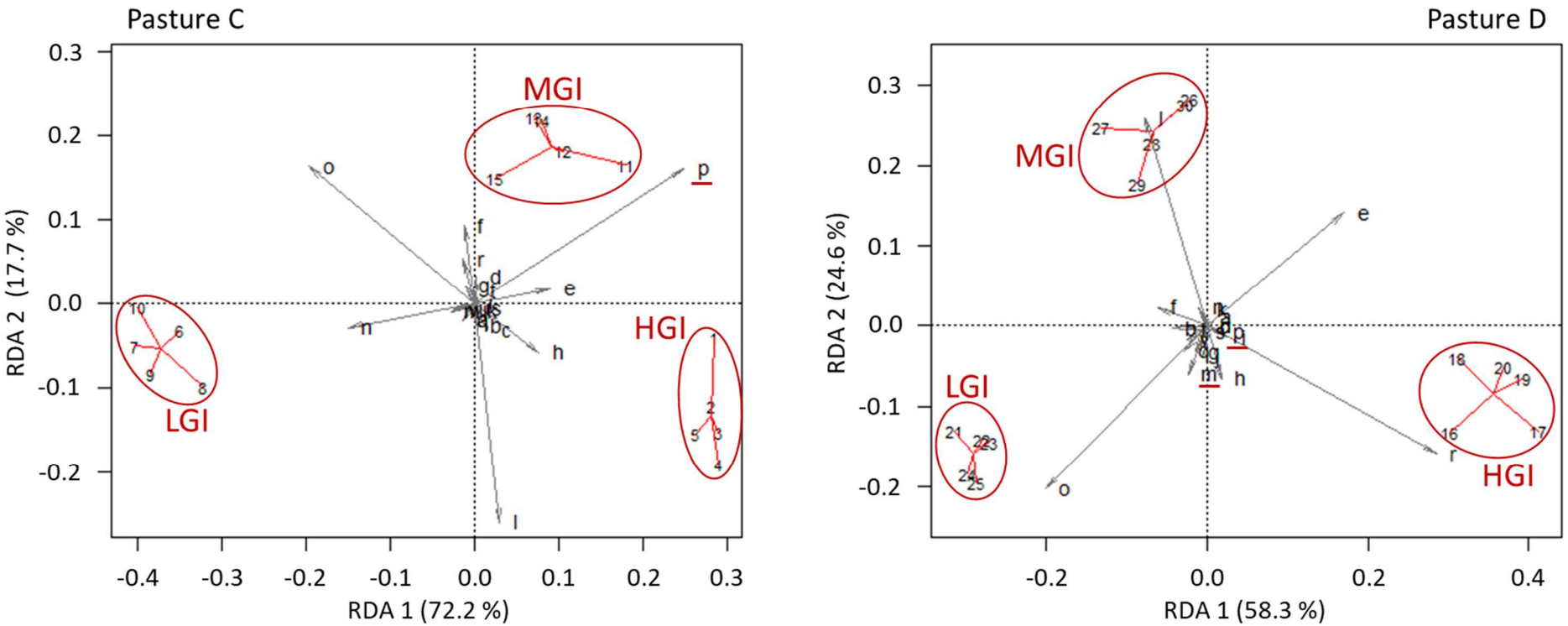

Figure 3. Triplots of RDA-based MANOVAs for the two pastures (C and D) sampled in the Alps area. Numbers represent the traps, whose "wa" scores are related to the centroids of the grazing intensity factor (three levels: Low = LGI, Moderate = MGI and High = HGI) by means of straight lines, in scaling 1. Ellipses represent the three distinct grazing intensity levels in each pasture. Letters represent the species. The percentage of variation explained by the RDAs is shown for each axis. Underlined letters correspond to indicator species found in the IndVal analysis (Table 2): *Geotrupes stercorarius* (m), *Oromus alpinus* (p). See **Appendix D** for letters identifying the other species on the triplots.

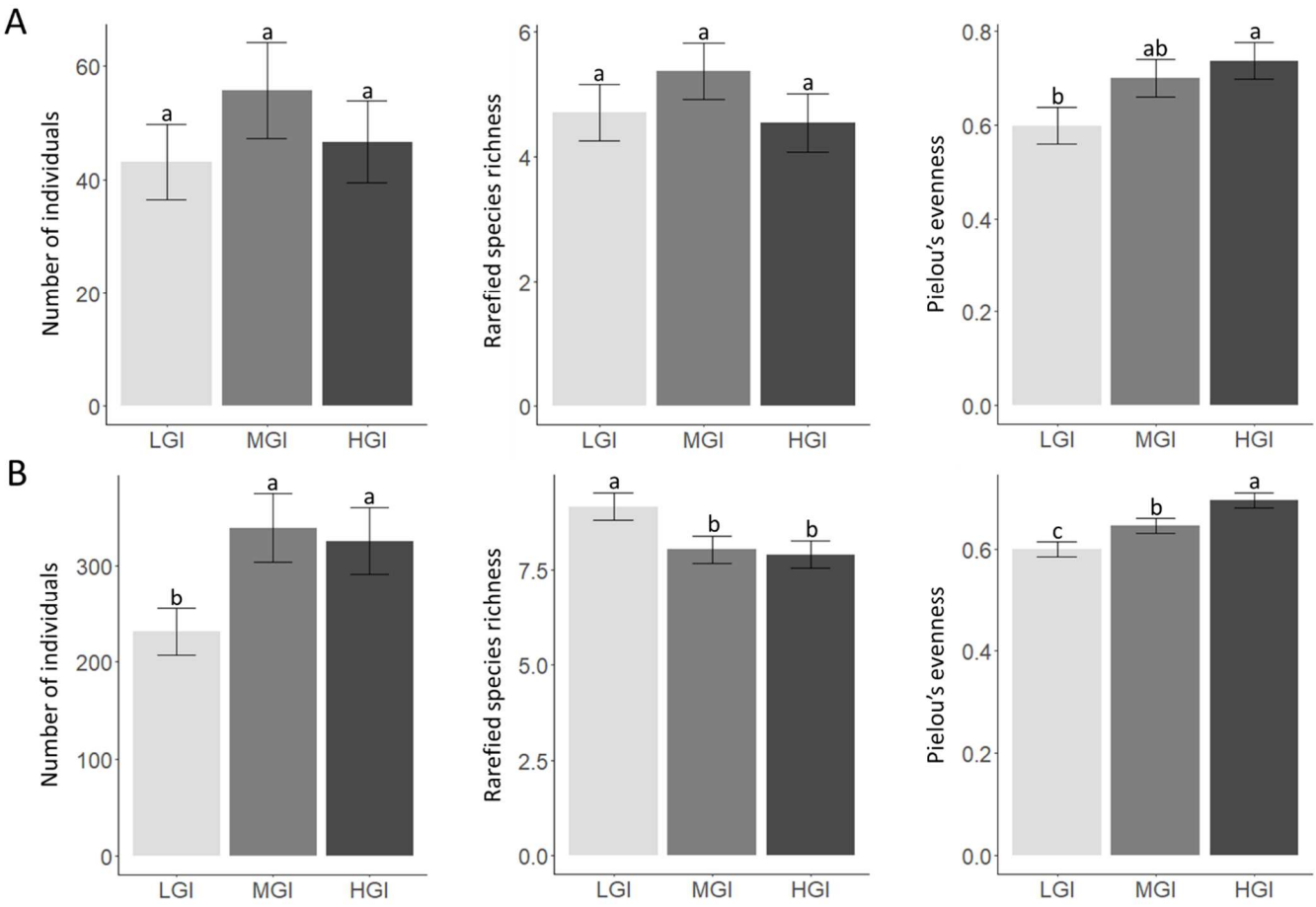

Figure 4. Variation in the number of individuals, rarefied species richness and Pielou's evenness between the three levels of grazing intensity in the steppe (A) and the Alps (B). Different letters (a, b, c) indicate significant differences between grazing intensity levels at $\alpha = 0.05$ based on the models. Vertical bars represent standard errors produced by the generalized linear models with a negative binomial family (for the number of individuals) and linear models with a Gaussian family (for rarefied species richness and Pielou's evenness).

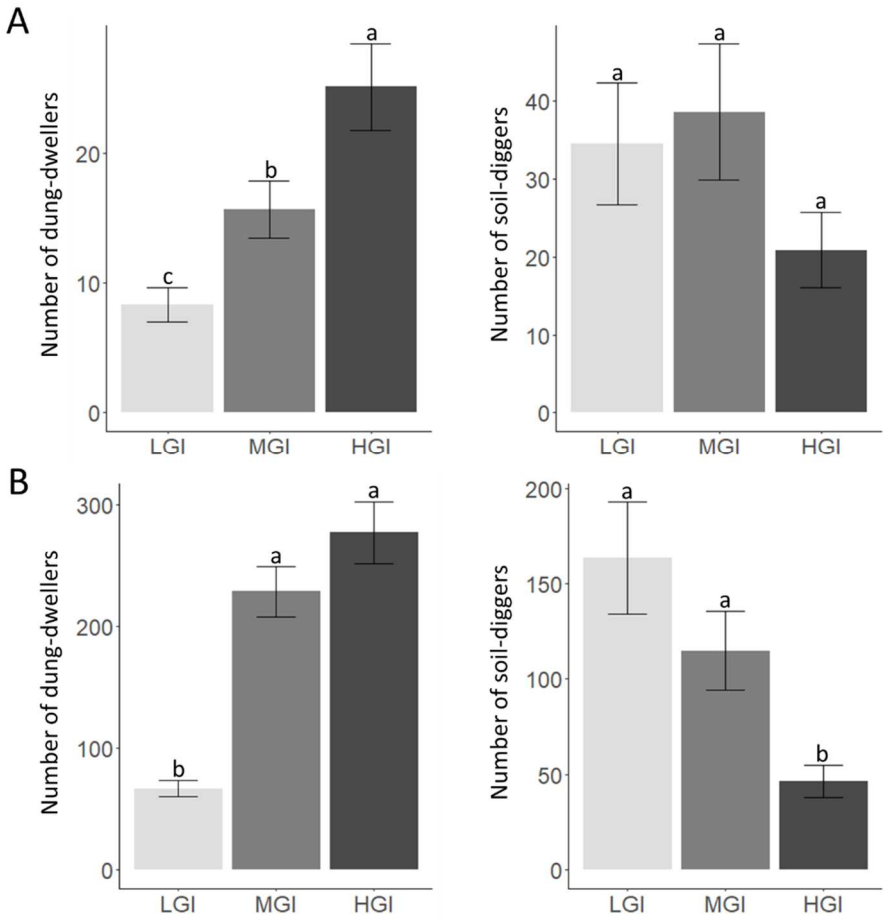

Figure 5. Variation in the number of dung-dwellers and soil-diggers between the three levels of grazing intensity in the steppe (A) and the Alps (B). Different letters (a, b, c) indicate significant differences between grazing intensity levels at $\alpha = 0.05$ based on the models. Vertical bars represent standard errors produced by the generalized linear models with a negative binomial family.

Table 1. Summarized statistics for dung beetles sampled in the steppe and the Alps. Mean values represent the mean number of individuals or species sampled per pitfall trap. *Percentage of species richness (in parentheses) inventoried according to estimates based on the iChao2 and ICE-1 indices.

Study area	Nb. indiv.	Mean indiv. ± SD	Nb. sp.	Mean sp. ± SD	iChao2 (%) *	ICE-1 (%) *
Steppe	1,465	48.8 ± 22.2	30	8 ± 3.0	40.2 (75)	35.8 (84)
Alps	10,268	342.3 ± 232.3	26	11.1 ± 2.3	26.4 (98)	28.2 (92)

Table 2. Results of the IndVal analysis with indicator species for each level of grazing intensity (GI) or combinations of two levels (Low–Moderate = LGI-MGI and Moderate–High = MGI-HGI). Only species with a significant IndVal value ($p \leq 0.05$) are shown. The values for specificity and fidelity are indicated, as well as nesting guild and mean dry body mass.

Steppe							
Grazing intensity	Species	Nesting guild	Mean body mass (mg) ± SD	Specificity	Fidelity	IndVal	p-Value
LGI	*Copris hispanus hispanus*	Soil-digger	452.2 ± 108.4	0.80	0.60	0.69	0.0052
LGI - MGI	*Onthophagus vacca*	Soil-digger	34.1 ± 5.0	0.94	1.00	0.97	0.0020
	Acrossus luridus	Dung-dweller	12.0 ± 2.8	0.92	0.70	0.80	0.0356
	Gymnopleurus flagellatus flagellatus	Soil-digger	67.7 ± 13.0	1.00	0.55	0.74	0.0104
	Euoniticellus fulvus	Soil-digger	13.8 ± 4.1	1.00	0.50	0.71	0.0262
	Eudolus quadrigutattus	Dung-dweller	2.8 ± 0.8	1.00	0.45	0.67	0.0400
MGI	*Onthophagus furcatus*	Soil-digger	4.9 ± 1.4	0.86	0.90	0.88	0.0002
	Caccobius schreberi	Soil-digger	9.1 ± 2.2	0.85	0.60	0.71	0.0118
MGI - HGI	*Onthophagus ruficapillus*	Soil-digger	6.4 ± 1.6	0.98	0.80	0.89	0.0020
HGI	*Calamosternus granarius*	Dung-dweller	3.1 ± 0.9	0.99	1.00	0.99	0.0002
	Aphodius foetidus	Dung-dweller	6.9 ± 2.4	0.95	0.60	0.76	0.0022
	Onthophagus opacicollis	Soil-digger	15.8 ± 3.0	1.00	0.50	0.71	0.0048
Alps							
Grazing intensity	Species	Nesting group	Mean body mass (mg) ± SD	Specificity	Fidelity	IndVal	p-Value
LGI	*Geotrupes stercorarius*	Soil-digger	163.5 ± 60.2	0.81	0.80	0.80	0.0006
	Trypocopris vernalis	Soil-digger	92.1 ± 26.2	0.83	0.70	0.76	0.0016
	Otophorus haemorrhoidalis	Dung-dweller	3.1 ± 1.0	0.78	0.60	0.68	0.0122
MGI - HGI	*Oromus alpinus*	Dung-dweller	3.1 ± 0.7	1.00	0.60	0.68	0.0190