

# 1 **The influence of fine-scale grazing heterogeneity on dung** 2 **beetle assemblages: what trait analysis teaches us**

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## 22 **Author Contributions**

23 WP and PJR conceived and designed the experiments. WP conducted the fieldwork. WP and  
24 LB made the trait measurements. WP, MM and SF analysed the data and discussed the results.  
25 WP wrote the first draft of the manuscript. WP, PJR, MM, SF and SC contributed to the  
26 discussion of the results and improved the manuscript. All authors gave final approval for  
27 publication.

28 **Abstract**

29 Livestock grazing puts major anthropogenic pressure on biological communities worldwide.  
30 Not all species are expected to be affected in the same way, and impact will depend on species'  
31 traits. Focusing on traits thus helps identify the mechanisms underlying changes in community  
32 composition under grazing pressures. We investigated how fine-scale grazing heterogeneity  
33 affects the trait composition and diversity of dung beetle assemblages in Western Europe. We  
34 sampled dung beetles in habitat patches differing in terms of grazing intensity within rangelands  
35 of two distinct biogeographical areas: a Mediterranean lowland steppe and Western alpine  
36 meadows. We measured five morphological traits expected to respond to the local-scale  
37 filtering pressure exerted by variations in grazing intensity. Using individual-based data, we  
38 assessed responses in terms of single-trait mean values in communities and complementary trait  
39 diversity indices. We found strong shifts in trait composition and diversity between the habitat  
40 patches. In both study areas, variations in habitat conditions are likely to have filtered the local  
41 occurrence and abundance of dung beetles by the mean of traits such as body mass (which have  
42 several functional implications), as well as traits linked to underground activity. We  
43 hypothesize that fine-scale variation in resource availability (i.e., droppings) and disturbance  
44 intensity (i.e., trampling) are key drivers of the observed patterns in species assemblages. Trait  
45 richness peaks at moderate grazing intensity in both study areas, suggesting that patches with  
46 an intermediated level of available resources and soil disturbance enables individuals with a  
47 greater range of autecological requirements to coexist.

48

49 Keywords: Alps, body size, Mediterranean, morphological traits, trait diversity

50

## 51 **Introduction**

52 Livestock farming is the dominant type of land use worldwide (Alkemade et al., 2013), thus  
53 understanding its impacts on ecosystems is of a great concern. In rangelands and pastures,  
54 livestock grazing greatly contributes to changes in vegetation and the associated animal  
55 community (Kruess and Tscharntke, 2002a; Cecil et al., 2019). Domestic ungulates can be  
56 considered as a source of disturbance (Hobbs, 2006), affecting the structure of various  
57 grassland-living animal communities through several processes, such as trampling, defecation,  
58 change in plant communities structure and plant biomass removal (Báldi et al., 2005; van Klink  
59 et al., 2015; Forbes et al., 2019; Val et al., 2019). These effects usually depend on the intensity,  
60 timing and duration of grazing, and on the ecological context (vegetation type and climate),  
61 which together mediate the livestock pressure on species communities (Milchunas and  
62 Lauenroth, 1993; de Bello et al., 2006; van Klink et al., 2015; Komac et al., 2015; Herrero-  
63 Jáuregui and Oesterheld, 2018; Török et al., 2018).

64 To study the ecological impacts of grazing, the scale of analysis also matters (Batáry et al.,  
65 2007; Cole et al., 2010; Wallis de Vries, 2016). A number of studies compared the structure  
66 and composition of natural communities between sites/parcels with distinct livestock densities  
67 (Kruess and Tscharntke, 2002a, 2002b; Batáry et al., 2007; Sjödin et al., 2008; Börschig et al.,  
68 2013; Tonelli et al., 2018, 2019). Within a pasture or rangeland, however, the flock's behaviour  
69 and its type of management are likely to lead to spatially heterogeneous grazing pressure at a  
70 finer scale (Wallis de Vries, 2016). This results in more or less heterogeneous soil conditions  
71 and vegetation structure (often dependent on the stocking rate), which in turn may influence the  
72 spatial occurrence of higher trophic levels within the grazed area (Kruess and Tscharntke,  
73 2002a; Cole et al., 2010; Jerrentrup et al., 2014). Although rarely considered, this scale of  
74 analysis is relevant especially for some taxonomic groups such as arthropods, which are  
75 sensitive to fine-scale variations in habitat conditions (Cole et al., 2010).

76 In order to understand the mechanism behind the effects of such environmental drivers at  
77 different spatial scales, investigating functional aspects of species and communities can be of  
78 great help. Species are characterised by functional traits, defined as any morphological,  
79 phenological, behavioural or physiological characteristics measurable at the individual level  
80 that impact fitness indirectly via their effects on growth, reproduction and survival (Violle et  
81 al., 2007). The value of these traits affects the capacity of a species to colonise and occupy  
82 habitat patches. By measuring the values of given traits that are predominant in a given

83 assemblage under given environmental conditions, one can infer which life-history strategies  
84 are selected under these conditions. For example, when sward is grazed short and bare soil is  
85 exposed, this often leads to an open habitat with warmer microclimate, which could be  
86 beneficial for the occurrence and development of various arthropods tolerant to high  
87 temperatures (Zhu et al., 2020), or taxa which need open areas to forage or deposit their eggs  
88 (Knisley, 2011). Patches of tall and dense vegetation, on the other hand, may cool temperatures,  
89 and support arthropods that deposit their eggs on or inside plants (van Klink et al., 2015). The  
90 pressure exerted locally by grazing is likely to influence the trait diversity of arthropod  
91 assemblages. Thus, focusing on the analysis of species' traits allows us to infer how species  
92 respond to grazing intensity (Zhu et al., 2020), and consequently how the trait composition  
93 influences the structure of species assemblages. Previous studies have demonstrated that high  
94 livestock intensity is likely to reduce functional diversity (i.e. diversity of trait values) of  
95 persisting plant species assemblages (Chillo et al., 2017) by constraining communities towards  
96 dominant species with stress tolerance or stress avoidance strategies (Díaz et al., 2007).  
97 However, very few studies have used functional traits to investigate animal responses to grazing  
98 practices, at least among arthropod communities. (e.g., Börschig et al., 2013; Chillo et al.,  
99 2017).

100 In addition, to changing vegetation, grazing ungulates also provide faeces used by many  
101 organisms for feeding or breeding. Among them, dung beetles (Aphodiinae, Scarabaeinae,  
102 Geotrupinae) constitute one of the most characteristic taxonomic groups in grazed landscapes  
103 (Hanski and Cambefort, 1991). Most dung beetles use active flight to exploit ephemeral and  
104 patchily distributed dung pads, and display a wide range of feeding and breeding strategies that  
105 contribute to the reduction of competition between co-occurring species (Halffter and Edmonds,  
106 1982). Some species develop entirely inside the dung or at the soil-dung interface (dwellers),  
107 while others relocate dung fragments for feeding and breeding, either building tunnels under  
108 dung pads (tunnelers) or rolling dung balls some distance from the excrement (rollers) (Hanski  
109 and Cambefort, 1991; Gittings and Giller, 1997). In temperate regions, soil-nesting species have  
110 generally lower reproductive rate than dwellers, which is compensated by a higher level of  
111 parental care.

112 In Europe and around the Mediterranean, dung beetles strongly react to land use change and  
113 resource availability following changes in livestock farming practices (Lumaret et al., 1992;  
114 Jay-Robert et al., 2008c; Buse et al., 2015; Errouissi and Jay-Robert, 2018; Tonelli et al., 2018,  
115 2019; Cuesta and Lobo, 2019). By comparing sites with distinct levels of stocking rates, studies

116 showed that a gradual abandonment of traditional grazing practices could be detrimental  
117 especially for species with large body size, but also to species with a dung-dwelling behaviour  
118 (Tonelli et al., 2018, 2019). To date, little attention has been paid to the effects of fine-scale  
119 variations of grazing intensity within pastures, while this scale of analysis can improve our  
120 understanding of dung beetle responses to grazing intensity. Moreover, some authors recently  
121 demonstrated that (i) describing the dung beetle phenotype as a combination of continuous  
122 morphological traits is likely to be a good surrogate for the ecological diversity of dung beetle  
123 species assemblages; and (ii) this may allow us to improve our comprehension of the  
124 mechanisms behind their responses to environmental pressures (Inward et al., 2011; Pessôa et  
125 al., 2017; Raine et al., 2018; Hosler et al., 2020). The eco-morphological approach, which  
126 postulates that morphological traits are an important manifestation of the niche position of  
127 species within a community (Ricklefs and Travis, 1980; Wainwright and Reilly, 1994), should  
128 thus provide a relevant method to investigate the effects of grazing intensity on dung beetle  
129 species assemblages.

130 In the present study, we hypothesize that spatially heterogeneous grazing intensity within  
131 grazed sites may have an effect on the local occurrence of dung beetle species and therefore on  
132 the functional structure of species assemblages at a fine scale. We specifically address the two  
133 following questions: 1) Which traits reflect the response of dung beetles to fine-scale grazing  
134 heterogeneity? 2) Does grazing act as an environmental filter that induces variation in the trait  
135 diversity of local dung beetle species assemblages? By studying continuous morphological  
136 traits, we expected that fine-scale variations in grazing intensity would be reflected by changes  
137 in the morphological trait space occupied by dung beetle communities.

138 To address these questions, we selected rangelands of two distinct bioclimatic areas in France:  
139 (i) a Mediterranean semi-arid lowland steppe, and (ii) 2000-m-altitude mountain meadows in  
140 the French Alps. This allowed us to compare grazing effects on dung beetle communities with  
141 radically distinct taxonomic composition (Lumaret and Stiernet, 1991; Tatin et al., 2014; Perrin  
142 et al., 2019), thus testing whether traits reveal general response patterns to environmental  
143 changes. In these two areas, we studied two sites consisting of rangelands with a long-term  
144 grazing history, where shepherds graze their flocks. This traditional livestock management  
145 allowed us to compare dung beetle species assemblages between habitat patches created under  
146 spatially heterogeneous grazing intensity within all sites. This fine-scale heterogeneity in  
147 grazing intensity was expected to produce local environmental filters, namely distinct levels of  
148 livestock-induced disturbances (e.g., soil compaction, removal of the herbaceous layer) and

149 variations in dung availability, both expected to induce changes in dung beetle assemblage  
150 composition and diversity.

151

## 152 **Materials and Methods**

### 153 **Study areas and sampling design**

154 We carried out our study in rangelands of two protected areas in France that are highly distinct  
155 in terms of bioclimatic conditions: the Coussouls de Crau National Nature Reserve (hereafter,  
156 ‘the steppe’) and the Vanoise National Park (hereafter, ‘the Alps’) (Supplemental Material S1,  
157 Figure S1.1). The steppe is a vast area of dry grasslands (11,000 ha) located near the  
158 Mediterranean Sea (43°33’N, 4°51’E) at an altitude of less than 50 m a.s.l. (Tatin et al., 2013).  
159 The climate is typically Mediterranean, with a dry season in summer, and two periods of rainfall  
160 in spring and autumn (mean annual temperature: 14 °C; mean annual rainfall: 540 mm). In this  
161 semi-arid steppe, sheep grazing is a tradition that dates back centuries. Today, some 40,000  
162 sheep still graze the plain from the end of winter to early summer (Tatin et al., 2013). The  
163 grazing activity is organized in a patchwork of 70 contiguous rangelands through which a  
164 shepherd conducts its flock.

165 The Alps study area is located in the Western Alps (45°14’N, 6°43’E) and has a typical alpine  
166 climate, with snowy winters and mild summers (mean annual temperature: 9.5 °C; mean annual  
167 rainfall: 965 mm; internal data Vanoise National Park). Every year 61,000 sheep graze the  
168 subalpine meadows of the Vanoise National Park, following a transhumant cycle, which entails  
169 bringing herds up to high-altitude pastures in early summer and moving them down to the  
170 valleys and plains in autumn (Cleary et al., 1987).

171 We selected two distinct sites (i.e., two distinct rangelands) in each study area, locally named  
172 ‘Petit Carton’ and ‘Grosse du Couchant’ in the steppe, and ‘Aussois’ and ‘Barbier’ in the Alps  
173 (Supplemental Material S1, Figure S1.2). All sites have a long-term grazing history,  
174 experiencing uninterrupted grazing for at least 190 years in the steppe, and at least 68 years in  
175 the Alps (according to information provided by local range managers). The two sites in each  
176 respective area are 6.2 km apart in the steppe and 3.2 km apart in the Alps. Within each area,  
177 the sampled rangelands were characterized by a single grassland habitat dominated by  
178 herbaceous species (steppe: phytosociological association *Asphodeletum fistulosii* dominated  
179 by *Brachypodium retusum* (Pers.) P.Beauv., *Thymus vulgaris* L. and *Asphodelus ayardii*

180 Jahand. & Maire; Alps: mesophile deep soil *Patzkea paniculata* (L.) G.H.Loos swards;  
181 CORINE Biotopes classification by Devillers et al. (1991)) and had a similar soil type (steppe:  
182 compacted clay soil from alluvial deposits of the paleo-Durance River; Alps: silica and silicate-  
183 rich substrates from crystalline rocks). One distinct sheep flock grazed each site during a four-  
184 month period on average each year (March–June in the steppe and June/ July–October in the  
185 Alps).

186 Within each site, we used three patches characterized by different grazing intensity (hereafter,  
187 ‘GI’) levels: low grazing intensity (LGI), moderate grazing intensity (MGI) and high grazing  
188 intensity (HGI) (Supplemental Material S1, Figure S1.2). Within a site, the GI patches were  
189 separated by at least 170 m (minimizing undesirable interaction between species assemblages  
190 occurring in these patches (Larsen and Forsyth, 2005) (Supplemental Material S2, Tables S2.1,  
191 S2.2). To identify these GI patches, we relied on the current livestock management method used  
192 by local shepherds and sheep breeders, and used a method of characterisation of these patches  
193 as consistent as possible between the rangelands of the two studied areas. LGI patches were  
194 located at the edge of pastures, where shepherds lead their flocks occasionally or at low  
195 frequency (Dureau and Bonnefon, 1998), resulting in low sheep dropping availability and low  
196 livestock-induced pressure on soil and on the herbaceous layer. MGI patches were located in  
197 the main grazing areas, where shepherds regularly lead their flocks throughout the grazing  
198 season. HGI patches were located within or near the flock’s overnight sites, characterized by  
199 intensive grazing and repeated trampling (both extending the areas of bare soil and potentially  
200 increasing soil compaction) and by a high load of droppings. In the Alps, these patches are  
201 relatively small outdoor fenced enclosures. In the steppe, most of the pastures benefit from a  
202 sheepfold in which the flock is kept during the night. The livestock pressure around these  
203 sheepfolds is especially high (Tatin et al., 2013), and was expected to be comparable to that  
204 inside the enclosures in alpine pastures. Recently, Génin et al. (2021) well described the grazing  
205 intensity gradient in the Crau steppe by demonstrating an increase of the percentage of ruderal  
206 plants, soil nitrogen, dung coverage and patches of bare soil from the edges of rangelands to  
207 the vicinity of sheepfolds. In one of the steppe pastures, ‘Grosse du Couchant’, the sheepfold is  
208 too small for the flock, and sheep stay overnight in a fenced enclosure. In the ‘Petit Carton’  
209 steppe pasture, the HGI patch was located in the neighbourhood of the sheep resting place (i.e.,  
210 the sheepfold), because the sheepfold itself provides unsuitable living conditions for dung  
211 beetles. As each site contained only one overnight site (i.e., one HGI patch available to sample),  
212 it was not possible to replicate the different grazing conditions within a rangeland. Once these

213 GI patches were defined, we validated them by measuring the maximum height of herbaceous  
214 vegetation (indicator previously used by Evans et al. (2015) and Mohandass et al. (2016) to  
215 characterize grazing intensity) and the amount of sheep droppings in each GI patch (one  
216 sampling during the grazing season). The results showed that the maximum height of  
217 herbaceous vegetation significantly decreased, while the amount of sheep droppings  
218 significantly increased with increasing GI (Table 1 and Supplemental Material S3, Figures S3.1,  
219 S3.2).

220

## 221 **Dung beetle sampling**

222 Within each LGI, MGI and HGI patch in each of the four sites (*'Petit Carton'* and *'Grosse du*  
223 *Couchant'* in the steppe, *'Aussois'* and *'Barbier'* in the Alps), we collected dung beetles using  
224 five pitfall traps exposed for 72 hours on sunny days. We used the CSR (Cebo-Suspendido-  
225 Rejilla) model described by Veiga et al. (1989): the traps consisted of plastic basins (Ø 20 cm,  
226 depth 15 cm) buried to the rim in the soil, filled with water and a few drops of neutral soap, and  
227 covered with a grid (mesh size between 4 cm<sup>2</sup> and 16 cm<sup>2</sup>) on top of which we placed  
228 approximately 300 g of fresh sheep droppings. Using this method in Southern France, Lobo et  
229 al. (1998) demonstrated that 10 traps over 48 hours allowed the collection of more than 70% of  
230 the species present within 1 km<sup>2</sup>, thus giving a reasonable picture of the composition of the  
231 local dung beetle community. Overall, 60 pitfall traps were set up in our study (5 per level of  
232 GI x 3 GI levels x 2 sites x 2 areas). In all the studied rangelands, HGI patches had a small  
233 surface area (less than 5,000 m<sup>2</sup>). Thus, in order to sample a habitat as homogeneous as possible  
234 in terms of GI, and to standardize the sampling design for all GI patches, we placed the traps  
235 10 m apart in accordance with the standard design used in temperate contexts (e.g., Lobo et al.,  
236 2001, 2006; Jay-Robert et al., 2008a, 2008b). We targeted the period when dung beetle species  
237 richness is highest in the Mediterranean region (April, spring) and in high-altitude meadows  
238 (end of July – beginning of August, summer) (Jay-Robert et al., 2008a, 2008b), in 2018 and  
239 2017 respectively. Although the sampling was not exhaustive, previous studies have shown that  
240 the dung beetle inventory of a local assemblage, when recorded at the peak of activity, ranged  
241 from 70% to 80% of the complete annual inventory (Martin-Piera et al., 1992; Lobo and Martín  
242 Piera, 1993; Lobo et al., 1997). We identified all the captured specimens to species level using  
243 the taxonomic key provided by Paulian and Baraud (1982) for French dung beetles. The



244 voucher collection of all identified individuals are stored at the laboratory of the University  
245 Paul-Valéry Montpellier 3, France.

246

## 247 **Dung beetle morphological traits**

248 The common strategy for analysing functional traits is to use trait values from literature or  
249 databases. However, because species' traits (including morphological ones) may show some  
250 variation according to the biogeographical area where the organisms live, it is recommended to  
251 use a location-specific trait dataset (Bonfanti et al., 2018). In this study, we thus decided to  
252 describe the species we sampled with individual-based measurements, because in dung beetles  
253 interspecific differences explain the majority of variability in measured morphological traits  
254 (between 94% and 96%) (Griffiths et al., 2016). Recently developed indices make the  
255 integration of intraspecific trait variation in trait-based studies possible (e.g., Carmona et al.,  
256 2016; Fontana et al., 2016). We selected a maximum of 10 individuals per species (in some  
257 species less than 10 were available), resulting in a total of 333 measured individuals (**cf.**  
258 **Statistical Analysis**). We removed nine singleton species from our dataset in order not to give  
259 too much importance to very rare species, thus retaining 43 species. We also prioritized the  
260 selection of females to reduce variability resulting from the strong sexual dimorphism present  
261 in some species, which may lead to high intraspecific variation.

262 For each individual, five traits were analysed using the following seven measures: dry body  
263 mass, pronotum length, pronotum width, elytra length, front tibia length, front tibia width, and  
264 back tibia length. Dry body mass was determined after drying beetles at 70 °C for 24 h, using  
265 a Sartorius CPA1245S analytical balance (Sartorius, Göttingen, Germany) with precision to  
266 0.001 g. The other measurements were made with a Leica MZ75 microscope and Leica  
267 Application Suite V4.12 software (Leica, Wetzlar, Germany). We selected the right side for leg  
268 measurements, although the left side was used if the right side was damaged. We combined  
269 four of the morphological measures we made by calculating ratios: back tibia *to* front tibia  
270 length, front tibia width *to* front tibia length, pronotum width *to* pronotum length, and pronotum  
271 length *to* pronotum + elytra length (**Table 2**). We used the sum of pronotum length + elytra  
272 length as a proxy for body size (Radtke and Williamson, 2005). These four ratios along with  
273 individuals' body mass were the five traits we subsequently used to calculate the different trait-  
274 based metrics. These traits are related to dispersal, nesting behaviour and resource use (e.g.,  
275 Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Griffiths et al., 2015; Pessôa et al.,

276 2017; Raine et al., 2018), and were therefore expected to respond to variations in grazing  
277 intensity (see **Table 2** for details).

278

## 279 **Trait-based metrics**

280 A bootstrap procedure was used to standardize across traps the number of individuals used to  
281 calculate the trait-based metrics. This is a crucial step, as it allows us to obtain trait diversity  
282 metrics that are independent of dung beetle abundance and thus suited to testing our hypotheses.  
283 In other words, we made sure that the observed trait diversity changes (especially in trait  
284 richness, which is particularly affected by the number of individuals) were not trivially driven  
285 by variation in dung beetle abundance across sites. Therefore, using all individual  
286 measurements available, we bootstrapped 10 individuals 999 times (whenever possible from  
287 the right combination of study area, site identity and GI). For two species, it was necessary for  
288 some traps to use traits measured in a different study area but under the same GI. For ten species,  
289 measurements were needed from the same pasture but under a different GI.

290 The probability of selecting a given measured individual was determined by the relative species  
291 abundance in each trap (i.e., the number of bootstrapped individuals of a given species was  
292 proportional to its relative abundance in the target community). Intraspecific trait variability  
293 was adequately taken into account (with the highest resolution available, which was different  
294 for each species) by repeating the calculations 999 times. We used the mean of the bootstrapped  
295 values of each trait-based metric for each trap in the statistical analyses.

296 Different facets of trait-based analyses provide complementary insights into the response of  
297 communities to changes in environmental conditions. The mean value of single traits in a  
298 community is commonly used to investigate the reshuffling of community trait composition in  
299 response to various gradients (Lavorel et al., 2008). In nature, however, species' responses to  
300 environmental gradients are expected to be determined by the response of several traits that  
301 may covary or show trade-offs (Reich et al., 2003). Indices based on multiple traits of species  
302 or individual organisms have thus been developed to describe the trait diversity of communities,  
303 and allow obtaining a comprehensive description of the processes structuring them along  
304 various gradients (Mouillot et al., 2013). In this study, we considered single trait and multiple  
305 trait approaches simultaneously.

306 We first investigated the trait composition of dung beetle communities by calculating the mean  
307 of each single trait (Table 2). We then quantified the trait diversity of dung beetle communities  
308 using three independent and complementary multiple-trait indices. TOP (trait onion peeling;  
309 Fontana et al., 2016) was used to measure trait richness, TED (trait even distribution; Fontana  
310 et al., 2016) was used to measure trait evenness, and FDis (functional dispersion; Laliberté and  
311 Legendre, 2010) was used to measure trait divergence. To avoid the inclusion of correlated  
312 traits in the calculation of trait diversity indices (Naeem and Wright, 2003), we checked for  
313 correlations between the different traits (Supplemental Material S4). The ratio ‘pronotum width  
314 to pronotum length’ was found to correlate quite strongly with dry body mass (Pearson’s  $r$  of  
315 0.58). We therefore decided to remove dry body mass from the calculation of multiple-trait  
316 indices, thus retaining the following ratios: back tibia to front tibia length, front tibia width to  
317 front tibia length, pronotum width to pronotum length, and pronotum length to pronotum +  
318 elytra length. The maximum pairwise correlation between these four morphological traits was  
319 0.44, which we considered as an acceptable level of correlation.

320 TOP is the sum of all successive convex hull areas touching the individuals of a community in  
321 a multidimensional trait space. It increases with the addition of unique trait values in the  
322 multidimensional trait space, and it is sensitive to the addition/exclusion of trait values located  
323 both in the middle and at the edges of the trait distribution (Fontana et al., 2016). TED measures  
324 the regularity in the distribution of individuals within the multidimensional trait space as  
325 compared to a perfectly even reference distribution. Continuous variation in TED can signal  
326 that organisms are converging around certain trait combinations (low TED, following data  
327 clustering), or spreading more regularly in the trait space (higher TED). FDis is the mean  
328 distance of individuals to the centroid of trait distribution. It increases when most organisms in  
329 a community possess highly different trait combinations. Decrease in trait richness and  
330 divergence may reflect the decrease or disappearance of unviable phenotypes in a community  
331 under environmental filtering (Cornwell et al., 2006; Mouillot et al., 2013, Fontana et al., 2016).  
332 Trait evenness is, in contrast, considered to be a measure of niche partitioning, and is therefore  
333 expected to increase when resource scarcity results in a low niche overlap across multiple trait  
334 dimensions as a means of avoiding competition (Fontana et al., 2018, 2019; He et al., 2018).

335

## 336 **Statistical analyses**

337 We assessed the effects of the factor ‘grazing intensity’ (LGI, MGI, HGI) on the three  
338 multidimensional trait-based metrics and on the mean of single traits (calculated for each pitfall  
339 trap) using standard linear models. Given that our aim was to compare the response of dung  
340 beetle communities to grazing between the two study areas, we fitted the models separately for  
341 the steppe and the Alps. Our sampling design featured two nested levels: two study areas (steppe  
342 and Alps) with two pastures each. The identity of the sampled pastures in each area could be  
343 considered as a random factor. However, the number of independent pastures in both the steppe  
344 and the Alps (two in each) was insufficient to accurately estimate group-level variation (Gelman  
345 and Hill, 2006). As a result, we used standard linear models, considering ‘pasture identity’ as a  
346 fixed effect. We interpreted the results by focusing on the ‘grazing intensity’ effect.

347 We performed all analyses in R (version 3.6.0, R Development Core Team 2019). We used the  
348 R script provided by Fontana et al. (2016) to compute TOP and TED, and the R package ‘FD’  
349 (Laliberté and Legendre, 2010) (*dbFD* function) to compute FDis.

350

## 351 **Results**

352 We collected a total of 11,727 dung beetles belonging to 50 species (see Supplemental Material  
353 S5 for a full species list with abundances recorded in each GI patch, site and study area). By  
354 comparison with previous inventories, our sampling design allowed us to have a good  
355 representation of the composition of local dung beetle communities in each study area  
356 (Supplemental Material S6). The species composition in the two study areas was very different,  
357 with only four Aphodiinae species in common (*Aphodius cardinalis* Reitter, *Calamosternus*  
358 *granaries* L., *Colobopterus erraticus* L. and *Otophorus haemorrhoidalis* L.). Species richness  
359 was slightly higher in the steppe compared to the Alps (28 vs 26), but the mean number of  
360 captured individuals in traps was seven times higher in the Alps (Mean  $\pm$  SE: steppe = 48.8  $\pm$   
361 4.0; Alps = 342.3  $\pm$  42.4).

362

### 363 **Changes in mean trait values in response to grazing intensity**

364 Mean trait values changed significantly between the GI patches and often similarly between the  
365 two study areas (Figure 1). Both in the steppe and the Alps, dung beetles in LGI patches were,  
366 on average, larger than those in HGI patches (steppe [LGI>HGI]:  $t = -9.02$ ,  $p < 0.001$ ; Alps  
367 [LGI>HGI]:  $t = -6.54$ ,  $p < 0.001$ ) (Figures 1a, 1f) and had broader pronotum (steppe

368 [LGI>HGI]:  $t = -5.19$ ,  $p < 0.001$ ; Alps [LGI>HGI]:  $t = -6.04$ ,  $p < 0.001$ ) (Figures 1c, 1h). In the  
369 steppe, dung beetles had a larger-proportioned pronotum relative to their size in LGI and MGI  
370 patches ([LGI>HGI]:  $t = -5.02$ ,  $p < 0.001$ ; [MGI>HGI]:  $t = -3.61$ ,  $p < 0.001$ ) (Figure 1b), while  
371 no significant variation was found for this trait in communities in the Alps (Figure 1g).  
372 Observed changes for leg-related traits in species assemblages were quite similar between the  
373 steppe and the Alps. Dung beetles in LGI patches had, on average, proportionately longer front  
374 tibiae compared to back tibiae (steppe [LGI<HGI]:  $t = 4.03$ ,  $p < 0.001$ ; Alps [LGI<HGI]:  $t =$   
375  $2.93$ ,  $p = 0.01$ ) (Figures 1d, 1i) and narrower front tibiae (steppe [LGI<HGI]:  $t = 4.83$ ,  $p <$   
376  $0.001$ ; Alps [LGI<HGI]:  $t = 2.75$ ,  $p = 0.01$ ) (Figures 1e, 1j) compared to dominant beetles in  
377 HGI patches which had proportionately longer back tibiae compared to the front tibiae, and  
378 shorter, broader front tibiae. Please refer to Table S7.1 (Supplemental Material S7) for statistical  
379 results for these comparisons, including estimates, df, t value and p value.

380

### 381 **Changes in trait diversity in response to grazing intensity**

382 We observed some significant changes in trait diversity values between the GI patches (Figure  
383 2). In both the steppe and the Alps, trait richness (TOP) peaked in MGI patches (steppe  
384 [MGI>LGI]:  $t = 2.84$ ,  $p = 0.01$ , steppe [MGI>HGI]:  $t = -2.66$ ,  $p = 0.01$ ; Alps [MGI>LGI]:  $t =$   
385  $3.00$ ,  $p = 0.01$ , Alps [MGI>HGI]:  $t = -2.61$ ,  $p = 0.01$ ) (Figures 2a, 2d). In the Alps, trait  
386 divergence (FDis) tends to be higher in species assemblages occurring in MGI patches  
387 [MGI>LGI]:  $t = 2.05$ ,  $p = 0.05$ , [MGI>HGI]:  $t = -2.81$ ,  $p = 0.01$ ) (Figure 2e), while no  
388 significant trend was observed in the steppe (Figure 2b). The results showed no significant  
389 trends in trait evenness (TED) between GI patches, both in the steppe and the Alps (Figure 2c,  
390 2f). Please refer to Table S7.2 (Supplemental Material S7) for statistical results for these  
391 comparisons, including estimates, df, t and p values.

392

### 393 **Discussion**

394 To date, only a few studies have addressed the responses of particular groups of arthropods to  
395 fine-scale heterogeneity in grazing intensity (e.g., Cole et al., 2010; Jerrentrup et al., 2014;  
396 Chillo et al., 2017). We found in this study that this scale of habitat patchiness matters for dung  
397 beetles. Because dung beetles are excellent fliers and actively forage for food by smell, they are  
398 able to move over long distances (Larsen and Forsyth, 2005; da Silva and Hernández, 2015),

399 exceeding those separating the different GI patches within the sampled rangelands (Cultid-  
400 Medina et al., 2015). Despite this long-distance foraging, we demonstrated in both the steppe  
401 and the Alps that fine-scale variations in grazing intensity are likely to result in changes in  
402 morphological trait composition and in trait diversity of dung beetles communities, specifically  
403 in terms of trait richness and trait divergence.

404

## 405 **How may the spatially heterogeneous grazing intensity influence dung beetle** 406 **assemblages at a fine scale?**

### 407 *Response of body mass*

408 In the two study areas, substantial – and often similar – changes in the mean trait values of dung  
409 beetle species assemblages were found between contrasting conditions in terms of grazing  
410 intensity within the studied rangelands. Among these changes, the observed decrease in dung  
411 beetle body mass with increasing grazing intensity may be explained by several non-mutually  
412 exclusive factors.

413 First, body mass – or body size more generally – is a central parameter in animal life histories,  
414 as it interacts with most fitness-related traits (Peters, 1983). A decrease in community mean  
415 body mass with increasing disturbance intensity has been demonstrated for several arthropod  
416 taxa (Simons et al., 2016; Wong et al., 2019). In dung beetles, differences in body size may be  
417 correlated with differences in behavior and fecundity, and such differences may explain the  
418 pattern observed for body mass, at least partially. Large dung beetles generally elaborate below  
419 ground nests in which the offspring find food and shelter (Hanski and Cambefort, 1991). This  
420 parental care compensates for the low fecundity of these species. To do their nest, adults of  
421 large species make numerous round trips between the ground and the surface to bury pieces of  
422 excrement; the entire nesting sequence may last from hours to several days (Klemperer, 1979,  
423 1982). One can hypothesize that repeated trampling of droppings in overgrazed areas might  
424 compromise the ability of these large species to make their nest efficiently. Smaller species  
425 (i.e., Aphodiinae species) that simply lay their eggs inside droppings or at the soil-dropping  
426 interface (Gittings and Giller, 1997) should be less disturbed. However, larvae of these small  
427 species should be more sensitive to an intensive trampling of their living substrate on the surface  
428 (i.e., droppings) than those living belowground (i.e., larvae of burrowing beetles). Therefore,  
429 the large offspring production by small species may allow the persistence of individuals in

430 overgrazed patches, contrary to large species - with few offspring - which are believed to be  
431 less adapted to highly disturbed habitats (Hanski and Cambefort, 1991).

432 Second, grazing intensity, by altering the structure of the vegetation, may modify prey  
433 detectability by predators (e.g., birds). Short vegetation height in highly grazed habitats has  
434 been associated with increased prey detectability (Butler and Gillings, 2004; Atkinson et al.,  
435 2004). It can therefore be hypothesized that droppings and associated dung beetles are more  
436 visible in short than in tall and dense vegetation. In line with this hypothesis, both in the steppe  
437 and the Alps, areas of bare soil in highly grazed habitats are frequently visited by several bird  
438 species, such as corvids (e.g., western jackdaw *Coloeus monedula* L., 1758, chough  
439 *Pyrrhocorax pyrrhocorax* L.) and passerines (e.g., wheatear *Oenanthe oenanthe* L.), which  
440 search for prey, including dung beetles in droppings (Young, 2015, and personal observations  
441 by WP). We note that dung beetle diversity can be relatively high on bare soil despite the  
442 presence of predatory birds (Sullivan et al., 2017a, 2017b). However, these studies focused on  
443 a homogeneous coastal dune ecosystem, while the habitat heterogeneity within our studied  
444 rangelands might create different selective pressures by predators such as birds at a small spatial  
445 scale (Vandenberghe et al., 2009; Murray et al., 2016). Increased predation in highly-grazed  
446 areas might preferentially affect large-bodied dung beetles that are more easily detected. This  
447 link between body size and predation pressure has been demonstrated for other prey types such  
448 as caterpillars (e.g., Rimmel and Tammaru, 2009), but remains to be tested in future studies for  
449 dung beetles.

450 Third, the observed decrease in dung beetle body mass with increasing grazing intensity might  
451 also be related to differences in dispersal capacity according to species' body size (Roslin,  
452 2000). Almost all dung beetle species living in temperate regions access feeding resources by  
453 flying and locating ephemeral dung patches thanks to their olfactory capacity (Tribe and Burger,  
454 2011). Larsen et al. (2008) showed that dung beetle body mass is highly positively correlated  
455 with wing loading (ratio of body mass to wing surface) and therefore flight performance (Le  
456 Roy et al., 2019). As a consequence, larger individuals with higher flight capacity are expected  
457 to be more efficient at acquiring the few and scattered resources available in the lightly grazed  
458 patches of rangelands. This pattern has already been reported in tropical environments, where  
459 large-bodied dung beetles are known to detect and access food from long distances (Nichols et  
460 al., 2013). Conversely, in a study conducted in Finland, Roslin (2000) found that small dung  
461 beetles mainly display 'dung pad-to-dung pad' dispersal patterns, a strategy expected to be more

462 efficient in highly grazed patches, with high resource density and large aggregation of sheep  
463 droppings.

464 Variations in dung density caused by changes in the level of grazing intensity may thus  
465 modulate the competitive interactions between dung beetles and may be an additional  
466 mechanism underlying the observed pattern. With their greater ability to access and rapidly  
467 garner large amounts of dung for nesting under low grazing intensity, larger species may  
468 prevent the use of droppings by smaller beetles through exploitative competition (Gittings and  
469 Giller, 1999). Conversely, the relaxation of competition with those large species in highly  
470 grazed patches may shift the competition balance in favor of smaller and non-nesting species  
471 (i.e., Aphodiinae), which may thus benefit from a greater amount of substrate for ovipositing  
472 and larval growth. Typically, some small Aphodiinae species can benefit from droppings  
473 accumulation in overgrazed areas (Lumaret and Iborra, 1996).

#### 474 ***Response of other morphological traits***

475 Our results also support our hypothesis that morphological traits related to soil-nesting  
476 strategies are filtered out at the higher grazing intensity. Dung beetles occurring in lightly  
477 grazed patches tended to have relatively elongated and longer-proportioned front tibiae  
478 compared to individuals at highly grazed patches, which had rather broad and shorter-  
479 proportioned front tibiae. More developed front legs can be considered a morphological  
480 adaptation for building underground nests while broader legs can help dwellers to progress in  
481 the soft mass of dung (Beutel et al., 2013). Thus, the observed pattern in the steppe and the Alps  
482 is likely to reflect a decrease in soil-living individuals within assemblages in highly grazed  
483 patches. This result is in line with the findings of Jankielsohn et al. (2001) and Negro et al.  
484 (2011) in intensively grazed areas of the African Savannah and the Italian Alps, respectively. It  
485 was suggested that this pattern is accounted for by repeated trampling that disrupts the physical  
486 characteristics of soil, creating unfavourable conditions for species that oviposit (e.g., in tiger  
487 beetles, Cornelisse and Hafernik, 2009) or build tunnels underground. In a recent study,  
488 Dabrowski et al. (2019) showed that South African dung beetles are able to dig and reproduce  
489 in highly compacted soils, but the effects of soil compaction may change depending on the  
490 species considered. However, presently little is known about the sensitivity of different  
491 European dung beetles to physically altered soil conditions. Measuring the soil hardness could  
492 have given us more information about this process; however, the very compact soil of the steppe  
493 prevented us to use the commonly applied tools (e.g., handheld penetrometer, Manning et al.



494 2016). We encourage future studies in explicitly exploring this link between soil physical  
495 disturbance due to trampling and the disappearance of soil digger dung beetles.

496 We also found that variations in grazing intensity selected particular trait values associated with  
497 the shape of the pronotum. In both study areas, dung beetles sampled in lightly and moderately  
498 grazed patches had, on average, a broader pronotum than those of highly grazed patches. In the  
499 steppe, they also had a larger-proportioned pronotum relative to the rest of the body. Given that  
500 an insect pronotum can be linked to several functions, two non-mutually exclusive hypotheses  
501 may explain the observed variation in pronotum shape. Firstly, this part of the body carries  
502 muscles attached for wing movement, and high flight speed requires strong musculature  
503 (Dickinson and Dudley, 2009). Therefore, individuals with the greatest flight performance  
504 usually have more developed pronotum (Attisano and Kilner, 2015). This supports our  
505 hypothesis that good flyers/dispersers dominate assemblages in lightly grazed patches where  
506 droppings are scarce. Secondly, since foreleg muscles are also located in this part of the body,  
507 individuals with larger pronotum should have a greater capacity to dig and move materials from  
508 underground to the soil surface (Table 2). Thus, the observed pattern may also result from the  
509 decrease in soil-digging beetles in highly grazed patches, in line with our hypothesis about leg-  
510 related traits.

511

## 512 **What are the consequences of those processes for trait diversity?**

513 The observed changes in morphological trait composition within dung beetle assemblages  
514 resulted in significant variations in some of the used multidimensional trait indices. In both the  
515 steppe and the Alps, dung beetle trait richness (TOP) is higher for species assemblages  
516 occurring in moderately grazed patches and decreased in the lightly and highly grazed ones.  
517 According to the theory of habitat filtering, environmental pressures are likely to filter  
518 organisms without suitable trait values to cope with local conditions (Cornwell et al., 2006;  
519 Pakeman, 2011). This may result in a reduced trait space, consisting of a restricted pool of the  
520 most adapted trait value combinations (Cornwell et al., 2006). In our study, specific  
521 morphological characteristics were selected at low and high grazing intensities. Specifically, as  
522 explained above, we suggest that livestock disturbance and high dropping density in intensively  
523 grazed patches selected mainly for small size and dweller species, while low disturbance  
524 intensity and resource availability in the lowest grazed patches selected for a restricted range of  
525 resource use strategies that enhance foraging efficiency. In moderately grazed patches,

526 intermediate levels of resource availability and disturbance intensity (i.e., disturbance of soil  
527 characteristics) may create a wider range of potential niches, allowing the local coexistence of  
528 individuals with different ecological requirements. This, in turn, might increase the  
529 morphological trait space occupied by dung beetle communities, and therefore results in the  
530 observed higher trait richness in moderately grazed patches. This hypothesis is in line with the  
531 results of Jerrentrup et al. (2014) and Pöyry et al. (2006) for other arthropods groups (e.g.,  
532 phytophagous insects), which had shown that species richness may peak at intermediate levels  
533 of sward height in temperate grasslands.

534 This selection of certain ecological strategies at high and low grazing intensity was also  
535 associated with lower trait divergence (FDis) in the Alps, probably because in these conditions  
536 certain trait combinations were filtered out towards the edges of the trait space. Consequently,  
537 most dung beetles living in these habitats displayed more homogeneous or similar trait  
538 combinations (as a consequence of trait filtering), leading to overall trait convergence in these  
539 dung beetles communities. Conversely, the heterogeneity of environmental conditions in  
540 moderately grazed patches facilitates the coexistence of numerous species with distinct  
541 ecological strategies, thus driving an increase in trait divergence (Jerrentrup et al., 2014).

542 This result, however, was not observed for species assemblages in the steppe, where we did not  
543 observe the same significant differences in trait divergence. More specifically, and contrary to  
544 the observed pattern in the Alps, steppe dung beetle assemblages occurring in highly grazed  
545 patches did not show a significantly reduced trait divergence compared to those sampled in  
546 moderately grazed patches. This result may be due to different sampling conditions between  
547 the two steppe study sites. Indeed, the presence of a sheepfold in the 'Petit Carton' pasture (see  
548 Material and methods - Study areas and sampling design) prevented us from sampling directly  
549 in the resting area. As a consequence, at 'Petit Carton', the HGI patch was sampled in the  
550 surroundings of the sheepfold, and showed FDis values that were significantly higher than those  
551 observed for the HGI of the second steppe rangeland (i.e., 'Grosse du Couchant') (respectively  
552 FDis mean  $\pm$  SE :  $1.52 \pm 0.05$  vs  $1.03 \pm 0.08$  ; Mann-Whitney test  $p = 0.01$ ). It is likely that,  
553 contrary to our expectations (see Material and methods - Study areas and sampling design),  
554 grazing intensity in the sheepfold 's surroundings was not as high as inside the outdoor resting  
555 place, with the result that the livestock-induced disturbance around the sheepfold was probably  
556 not strong enough to reduce trait divergence of the species assemblages, as was observed in  
557 other HGI patches.

558 Finally, trait evenness (TED) exhibited a distinct pattern compared to the trait richness and trait  
559 divergence, and we did not observe statistically significant variations for this index. As stated  
560 above, increasing TED is expected to result from competitive interactions reducing niche  
561 overlap. The absence of any clear tendency suggests that dung beetles are similarly tolerant to  
562 competition along the whole grazing intensity gradient covered in our study. In other words,  
563 the investigated gradients of disturbance and resource availability directly caused the  
564 disappearance of certain dung beetles (as discussed for trait richness and divergence), without  
565 necessarily causing niche partitioning among the viable phenotypes.

566

## 567 **Conclusions and perspectives**

568 Our study offers new insights into the effects of grazing intensity on arthropod communities in  
569 rangelands, with an emphasis on fine-scale processes, which have been poorly studied so far.  
570 Quite similar responses of dung beetle communities in a Mediterranean steppe and the French  
571 Alps validates the assumption that local environmental pressures can filter out dung beetles  
572 based on their trait combinations. Specifically, we found directional shifts in dung beetle body  
573 size and morphological traits, which we interpret as related to the fine-scale variations in  
574 dropping availability and soil conditions. Within rangelands, the reduction of filtering pressures  
575 in moderately grazed patches was found to increase trait richness within dung beetle species  
576 assemblages.

577 Dung beetles play a primary role in dung removal in grazed areas (Beynon et al., 2015), and  
578 how the variations in dung beetles assemblages reported in the present study alter this function  
579 remains to be explored. Because functionally richer assemblages are expected to be more  
580 efficient in performing dung removal (Milotić et al., 2017, 2019), variations in the functional  
581 structure of dung beetle assemblages are likely to alter this process. In overgrazed patches, our  
582 observations of dung accumulation could thus be linked to a decrease of both trait diversity and  
583 large species, which play a disproportionately important role in dung removal (Kaartinen et al.,  
584 2013; Milotić et al., 2017). Future studies are needed to confirm this hypothesis.

585 Finally, using sets of morphological traits allowed us to comprehensively investigate the effects  
586 of environmental pressures, as they affect the multidimensional phenotype that reflects an  
587 organism's niche (Ricklefs and Travis, 1980). However, for some taxa such as insects, the trait–  
588 environment relationship is still poorly understood. Moreover, many morphological features  
589 have multiple functional roles, and revealing how morphology differentially affects

590 performance – or whether such a causal relationship even occurs – can be difficult (Moen,  
591 2019). We, therefore, strongly recommend further laboratory and controlled experiments to  
592 assess the functional relevance of eco-morphological traits of dung beetle communities. This is  
593 a fundamental step towards improving predictive trait-based studies with terrestrial arthropods.

## 594 **Funding**

595 W.P. received a PhD grant from Paul Valéry University Montpellier III, France, and a  
596 supplementary grant from the same university to work at the Swiss Federal Institute for Forest,  
597 Snow and Landscape Research (WSL) in Birmensdorf, Switzerland. S.F. was supported by the  
598 Swiss National Science Foundation, Project 315230\_170200/1. The project also received  
599 financial support from the Vanoise National Park.

## 600 **Conflict of interests**

601 The authors declare that they have no conflict of interest.

## 602 **Ethical approval**

603 All procedures performed in studies involving human participants were in accordance with the  
604 ethical standards of the institutional and/or national research committee and with the 1964  
605 Helsinki declaration and its later amendments or comparable ethical standards. The capture and  
606 killing of insects (necessary to identify them) in the protected areas was allowed thanks to  
607 specific authorization given for our scientific study.

## 608 **Acknowledgements**

609 We thank the Biodiversity and Conservation Biology Research Unit of the WSL for their  
610 welcome. We are grateful to the staff at the Provence-Alpes-Côtes-d’Azur Conservatory of  
611 Natural Areas and the Vanoise National Park for their cooperation and assistance in this study.  
612 We thank the shepherds and sheep breeders for their cooperation.

613

614

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918 **Table 1.** Mean and standard error of maximum vegetation height (cm) and dung quantity (g.m<sup>-2</sup>) in GI  
 919 patches (LGI: Low Grazing Intensity, MGI: Moderate Grazing Intensity, HGI: High Grazing Intensity)  
 920 in the steppe and the Alps.

	Mean max. vegetation height (cm) ± SE			Mean dung quantity (g.m <sup>-2</sup> ) ± SE		
	LGI	MGI	HGI	LGI	MGI	HGI
<b>Steppe</b>	56.1 ± 5.7	25.6 ± 2.1	12.2 ± 1.6	3.1 ± 2.6	11.0 ± 3.8	56.2 ± 6.7
<b>Alps</b>	47.2 ± 3.9	33.3 ± 2.0	9.7 ± 1.1	0.0 ± 0.0	14.6 ± 4.2	146.1 ± 18.5

921

Table 2. Summary of the traits used to characterize the trait composition and diversity of dung beetle species assemblages. Please note that dry body mass was excluded for the calculation of multiple-trait indices. For each trait, we provide an interpretation key and information about its ecological relevance according to the literature. Under each trait, the denomination used in the results (Figure 1) is given.

Trait	Interpretation - Ecological relevance	Sources
<b>Dry body mass (in grams)</b> <i>Mean body mass (g)</i>	<p>The size of an individual. The higher the value, the larger the individual.</p> <p>Trait related to nutritional needs (requirement for adults and larvae), metabolic rate, dispersal capacity (correlated with wing loading) and reproductive rates (large species usually have lower fecundity).</p>	<p>Halffter and Edmonds, 1982  Hanski and Cambefort, 1991  Nichols and Gardner, 2011  Larsen et al., 2008  Nichols et al., 2013</p>
Ratio <b>Pronotum length to Body size</b> <i>Mean pron. length : body size</i>	<p>The proportion of the pronotum length compared to the whole body. The higher the value, the larger the pronotum compared to the body.</p> <p>The pronotum carries muscles associated with wings (related to flight performance) and legs (related to digging ability and dung manipulation). The abdomen (covered by elytra in beetles) is devoted to reproduction. A higher ratio may indicate a lower investment in reproduction compared to moving capacity.</p>	<p>Wickman and Karlsson, 1982  Attisano and Kilner, 2015  Pessôa et al., 2017</p>
Ratio <b>Pronotum width to Pronotum length</b> <i>Mean width : length pron.</i>	<p>The width of the pronotum compared to its length. The higher the value, the broader the pronotum.</p> <p>The muscles associated with wings occupy most of the pronotum cavity. A broader pronotum may contain thicker muscles and be associated with a better flight performance.</p>	<p>Attisano and Kilner, 2015  Pessôa et al., 2017</p>
Ratio <b>Back tibia length to Front tibia length</b> <i>Mean back : front tibia length</i>	<p>The length of the back tibia compared to the front tibia. The higher the value, the longer the back tibia compared to the front tibia.</p> <p>Soil-digging tunnelers are expected to present a smaller ratio than dung-dwelling species. Rollers have more developed back tibias.</p>	<p>Hanski and Cambefort, 1991  Inward et al., 2011</p>
Ratio <b>Front tibia width to Front tibia length</b> <i>Mean width : length front tibia</i>	<p>The width of the front tibia compared to its length. The higher the value, the broader and shorter the front tibia.</p> <p>More elongated front tibias might reflect a greater aptitude to move materials (dung, soil) from the soil surface to underground. Shorter and broader front tibias may be required to move within the pasty dung.</p>	<p>Hanski and Cambefort, 1991  Inward et al., 2011</p>

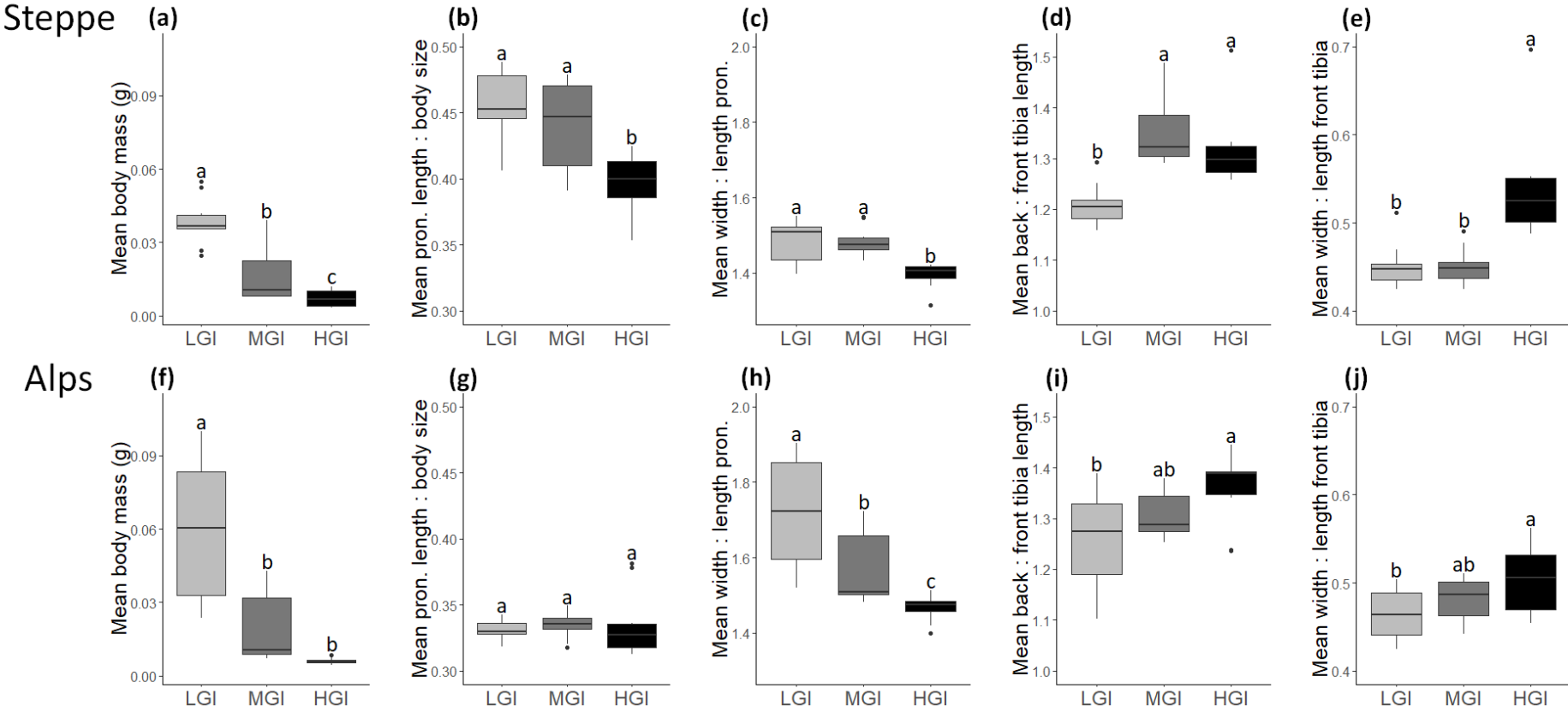


**Figure 1.** Variation in the mean value of each trait used in the analyses (**Table 2**) between the GI patches in the steppe (top row) and the Alps (bottom row). For each response variable, three levels of grazing intensity (GI) were tested: Low (LGI), Moderate (MGI), and High (HGI). Differing letters (a, b, c) indicate significant differences between grazing intensity levels at  $\alpha = 0.05$  based on the standard linear models (refer to Table S7.1 (Supplemental Material S7) for statistical results of the pairwise comparisons).

**Figure 2.** Variation in trait richness (TOP), trait divergence (FDis) and trait evenness (TED) in species assemblages between the GI patches in the steppe (top row) and the Alps (bottom row). For each response variable, three levels of grazing intensity (GI) were tested: Low (LGI), Moderate (MGI), and High (HGI). Differing letters (a, b, c) indicate significant differences between grazing intensity (GI) levels at  $\alpha = 0.05$  based on the standard linear models (refer to Table S7.2 (Supplemental Material S7) for statistical results of the pairwise comparisons).

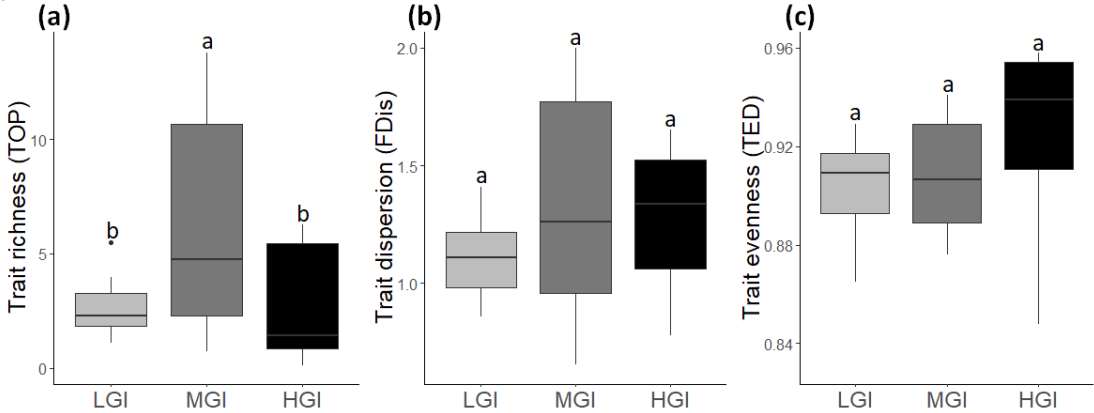


**Figure 1.**



**Figure 2.**

**Steppe**



**Alps**

