Environmental Entomology, 50(6), 2021, 1332–1343
https://doi.org/10.1093/ee/nvab091
Advance Access Publication Date: 28 September 2021
Research

Community Ecology

The Influence of Fine-Scale Grazing Heterogeneity on Dung Beetle Assemblages: What Trait Analysis Teaches Us

William Perrin,[1] Simone Fontana,[2,3] Sylvain Coq,[1] Laurent Berlioz,[1] Pierre Jay-Robert,[1] and Marco Moretti[2,4]

[1]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Université Paul Valéry Montpellier 3, Montpellier, France, [2]Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland, [3]Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany, and [4]Corresponding author, e-mail: marco.moretti@wsl.ch

Subject Editor: Richard Redak

Received 6 May 2021; Editorial decision 9 August 2021

Abstract

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

Key words: Alps, body size, Mediterranean, morphological trait, trait diversity

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

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

To understand the mechanism behind the effects of such environmental drivers at different spatial scales, investigating functional aspects of species and communities can be of great help. Species are characterized by functional traits, defined as any morphological, phenological, behavioral, or physiological characteristics measurable at the individual level that impact fitness indirectly via their effects on growth, reproduction, and survival (Violle et al. 2007). The value of these traits affects the capacity of a species to colonize and occupy habitat patches. By measuring the values of given traits that are predominant in a given assemblage under given environmental conditions, one can infer which life-history strategies are selected under these conditions. For example, when sward is grazed short and bare soil is exposed, this often leads to an open habitat with warmer microclimate, which could be beneficial for the occurrence and development of various arthropods tolerant to high temperatures (Zhu et al. 2020), or taxa which need open areas to forage or deposit their eggs (Knisley 2011). Patches of tall and dense vegetation, on the other hand, may cool temperatures, and support arthropods that deposit their eggs on or inside plants (van Klink et al. 2015). The pressure exerted locally by grazing is likely to influence the trait diversity of arthropod assemblages. Thus, focusing on the analysis of species' traits allows us to infer how species respond to grazing intensity (Zhu et al. 2020), and consequently how the trait composition influences the structure of species assemblages. Previous studies have demonstrated that high livestock intensity is likely to reduce functional diversity (i.e., diversity of trait values) of persisting plant species assemblages (Chillo et al. 2017) by constraining communities towards dominant species with stress tolerance or stress avoidance strategies (Díaz et al. 2007). However, very few studies have used functional traits to investigate animal responses to grazing practices, at least among arthropod communities. (e.g., Börschig et al. 2013, Chillo et al. 2017).

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

In Europe and around the Mediterranean, dung beetles strongly react to land use change and resource availability following changes in livestock farming practices (Lumaret et al. 1992, Jay-Robert et al. 2008c, Buse et al. 2015, Errouissi and Jay-Robert 2018, Tonelli et al. 2018, 2019, Cuesta and Lobo 2019). By comparing sites with distinct levels of stocking rates, studies showed that a gradual abandonment of traditional grazing practices could be detrimental especially for species with large body size, but also to species with a dung-dwelling behavior (Tonelli et al. 2018, 2019). To date, little attention has been paid to the effects of fine-scale variations of grazing intensity within pastures, while this scale of analysis can improve our understanding of dung beetle responses to grazing intensity. Moreover, some authors recently demonstrated that 1) describing the dung beetle phenotype as a combination of continuous morphological traits is likely to be a good surrogate for the ecological diversity of dung beetle species assemblages and 2) this may allow us to improve our comprehension of the mechanisms behind their responses to environmental pressures (Inward et al. 2011, Pessôa et al. 2017, Raine et al. 2018, Hosler et al. 2020). The eco-morphological approach, which postulates that morphological traits are an important manifestation of the niche position of species within a community (Ricklefs and Travis 1980, Wainwright and Reilly 1994), should thus provide a relevant method to investigate the effects of grazing intensity on dung beetle species assemblages.

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

To address these questions, we selected rangelands of two distinct bioclimatic areas in France: 1) a Mediterranean semi-arid lowland steppe and 2) 2,000-m-altitude mountain meadows in the French Alps. This allowed us to compare grazing effects on dung beetle communities with radically distinct taxonomic composition (Lumaret and Stiernet 1991, Tatin et al. 2014, Perrin et al. 2019), thus testing whether traits reveal general response patterns to environmental changes. In these two areas, we studied two sites consisting of rangelands with a long-term grazing history, where shepherds graze their flocks. This traditional livestock management allowed us to compare dung beetle species assemblages between habitat patches created under spatially heterogeneous grazing intensity within all sites. This fine-scale heterogeneity in grazing intensity was expected to produce local environmental filters, namely distinct levels of livestock-induced disturbances (e.g., soil compaction, removal of the herbaceous layer) and variations in dung availability, both expected to induce changes in dung beetle assemblage composition and diversity.

Materials and Methods

Study Areas and Sampling Design

We carried out our study in rangelands of two protected areas in France that are highly distinct in terms of bioclimatic conditions: the Coussouls de Crau National Nature Reserve (hereafter, 'the steppe') and the Vanoise National Park (hereafter, 'the Alps'; Supp Fig. 1.1 [online only]). 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 the Mediterranean, with a dry season in summer, and two periods of rainfall in spring and autumn (mean annual temperature: 14°C; mean annual rainfall: 540 mm). In this semi-arid steppe, sheep grazing is a tradition that dates back centuries. Today, some 40,000 sheep still graze the plain from the end of winter to early summer (Tatin et al. 2013). The grazing activity is organized in a patchwork of 70 contiguous rangelands through which a shepherd conducts its flock.

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

We selected two distinct sites (i.e., two distinct rangelands) in each study area, locally named 'Petit Carton' and 'Grosse du Couchant' in the steppe, and 'Aussois' and 'Barbier' in the Alps (Supp Fig. 1.2 [online only]). All sites have a long-term grazing history, experiencing uninterrupted grazing for at least 190 yr in the steppe, and at least 68 yr in the Alps (according to information provided by local range managers). The two sites in each respective area are 6.2 km apart in the steppe and 3.2 km apart in the Alps. Within each area, the sampled rangelands were characterized by a single grassland habitat dominated by herbaceous species (steppe: phytosociological association *Asphodeletum fistulosii* dominated by *Brachypodium retusum* (Pers.) P.Beauv. (Poales: Poaceae), *Thymus vulgaris* L. (Lamiales: Lamiaceae) and *Asphodelus ayardii* Jahand. & Maire (Asparagales: Asphodelaceae); Alps: mesophile deep soil *Patzkea paniculata* (L.) G.H.Loos (Poales: Poaceae) swards; CORINE Biotopes classification by Devillers et al. (1991)) and had a similar soil type (steppe: compacted clay soil from alluvial deposits of the paleo-Durance River; Alps: silica and silicate-rich substrates from crystalline rocks). One distinct sheep flock grazed each site during a four-month period on average each year (March–June in the steppe and June/July–October in the Alps).

Within each site, we used three patches characterized by different grazing intensity (hereafter, 'GI') levels: low grazing intensity (LGI), moderate grazing intensity (MGI), and high grazing intensity (HGI; Supp Fig. 1.2 [online only]). Within a site, the GI patches were separated by at least 170 m (minimizing undesirable interaction between species assemblages occurring in these patches (Larsen and Forsyth 2005; Supp Tables 2.1 and 2.2 [online only]). To identify these GI patches, we relied on the current livestock management method used by local shepherds and sheep breeders, and used a method of characterization of these patches as consistent as possible between the rangelands of the two studied areas. LGI patches were located at the edge of pastures, where shepherds lead their flocks occasionally or at low frequency (Dureau and Bonnefon 1998), resulting in low sheep dropping availability and low livestock-induced pressure on soil and on the herbaceous layer. MGI patches were located in the main grazing areas, where shepherds regularly lead their flocks throughout the grazing season. HGI patches were located within or near the flock's overnight sites, characterized by intensive grazing and repeated trampling (both extending the areas of bare soil and potentially increasing soil compaction) and by a high load of droppings. In the Alps, these patches are relatively small outdoor fenced enclosures. In the steppe, most of the pastures benefit from a sheepfold in which the flock is kept during the night. The livestock pressure around these sheepfolds is especially high (Tatin et al. 2013), and was expected to be comparable to that inside the enclosures in alpine pastures. Recently, Génin et al. (2021) well described the grazing intensity gradient in the Crau steppe by demonstrating an increase in the percentage of ruderal plants, soil nitrogen, dung coverage, and patches of bare soil from the edges of rangelands to the vicinity of sheepfolds. In one of the steppe pastures, 'Grosse du Couchant', the sheepfold is too small for the flock, and sheep stay overnight in a fenced enclosure. In the 'Petit Carton' steppe pasture, the HGI patch was located in the neighborhood of the sheep resting place (i.e., the sheepfold), because the sheepfold itself provides unsuitable living conditions for dung beetles. As each site contained only one overnight site (i.e., one HGI patch available to sample), it was not possible to replicate the different grazing conditions within rangeland. Once these GI patches were defined, we validated them by measuring the maximum height of herbaceous vegetation (indicator previously used by Evans et al. (2015) and Mohandass et al. (2016) to characterize grazing intensity) and the amount of sheep droppings in each GI patch (one sampling during the grazing season). The results showed that the maximum height of herbaceous vegetation significantly decreased, while the amount of sheep droppings significantly increased with increasing GI (Table 1 and Supp Figs. 3.1 and 3.2 [online only]).

Dung Beetle Sampling

Within each LGI, MGI, and HGI patch in each of the four sites ('Petit Carton' and 'Grosse du Couchant' in the steppe, 'Aussois' and 'Barbier' in the Alps), we collected dung beetles using five pitfall traps exposed for 72 hr on sunny days. We used the CSR (Cebo-Suspendido-Rejilla) model described by Veiga et al. (1989): the 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 (mesh size between 4 cm² and 16 cm²) on top of which we placed approximately 300 g of fresh sheep droppings. Using this method in Southern France, Lobo et al. (1998) demonstrated that 10 traps over 48 hr allowed the collection of more than 70% of the species present within 1 km², thus giving a reasonable picture of the composition of the local dung beetle community. Overall, 60 pitfall traps were set up in our study (5 per level of GI × 3 GI levels × 2 sites × 2 areas). In all the studied rangelands, HGI patches had a small surface area (less than 5,000 m²). Thus, to sample a habitat as homogeneous as possible in terms of GI, and

Table 1. Mean and standard error of maximum vegetation height (cm) and dung quantity (g.m^{-2}) in GI patches (LGI: Low Grazing Intensity, MGI: Moderate Grazing Intensity, HGI: High Grazing Intensity) in the steppe and the Alps

	Mean max. vegetation height (cm) ± SE			Mean dung quantity (g m^{-2}) ± SE		
	LGI	MGI	HGI	LGI	MGI	HGI
Steppe	56. 1 ± 5.7	25. 6 ± 2.1	12. 2 ± 1.6	3. 1 ± 2.6	11. 0 ± 3.8	56. 2 ± 6.7
Alps	47. 2 ± 3.9	33. 3 ± 2.0	9. 7 ± 1.1	0. 0 ± 0.0	14. 6 ± 4.2	146. 1 ± 18.5

to standardize the sampling design for all GI patches, we placed the traps 10 m apart in accordance with the standard design used in temperate contexts (e.g., Lobo et al. 2001, 2006, Jay-Robert et al. 2008a,b). We targeted the period when dung beetle species richness is highest in the Mediterranean region (April, spring) and in high-altitude meadows (end of July—beginning of August, summer; Jay-Robert et al. 2008a,b), in 2018 and 2017 respectively. Although the sampling was not exhaustive, previous studies have shown that the dung beetle inventory of a local assemblage, when recorded at the peak of activity, ranged from 70 to 80% of the complete annual inventory (Martin-Piera et al. 1992, Lobo and Martín Piera 1993, Lobo et al. 1997). We identified all the captured specimens to species level using the taxonomic key provided by Paulian and Baraud (1982) for French dung beetles. The voucher collection of all identified individuals are stored at the laboratory of the University Paul Valéry Montpellier 3, France.

Dung Beetle Morphological Traits

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

For each individual, five traits were analyzed using the following seven measures: dry body mass, pronotum length, pronotum width, elytra length, front tibia length, front tibia width, and back tibia length. Dry body mass was determined after drying beetles at 70°C for 24 hr, using a Sartorius CPA1245S analytical balance (Sartorius, Göttingen, Germany) with precision to 0.001 g. The other measurements were made with a Leica MZ75 microscope and Leica Application Suite V4.12 software (Leica, Wetzlar, Germany). We selected the right side for leg measurements, although the left side was used if the right side was damaged. We combined four of the morphological measures we made by calculating ratios: back tibia *to* front tibia length, front tibia width *to* front tibia length, pronotum width *to* pronotum length, and pronotum length *to* pronotum + elytra length (Table 2). We used the sum of pronotum length + elytra length as a proxy for body size (Radtke and Williamson 2005). These four ratios along with individuals' body mass were the five traits we subsequently used to calculate the different trait-based metrics. These traits are related to dispersal, nesting behavior, and resource use (e.g., Halffter and Edmonds 1982, Hanski and Cambefort 1991, Griffiths et al. 2015, Pessôa et al. 2017, Raine et al. 2018), and were therefore expected to respond to variations in grazing intensity (see Table 2 for details).

Table 2. Summary of the traits used to characterize the trait composition and diversity of dung beetle species assemblages

Trait	Interpretation - Ecological relevance	Source
Dry body mass (in g) *Mean body mass (g)*	The size of an individual. The higher the value, the larger the individual. 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).	Halffter and Edmonds 1982, Hanski and Cambefort 1991, Nichols and Gardner 2011, Larsen et al. 2008, Nichols et al. 2013
Ratio **Pronotum length *to* Body size** *Mean pron. length:body size*	The proportion of the pronotum length compared to the whole body. The higher the value, the larger the pronotum compared to the body. 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.	Wickman and Karlsson 1989, Attisano and Kilner 2015, Pessôa et al. 2017
Ratio **Pronotum width *to* Pronotum length** *Mean width:length pron.*	The width of the pronotum compared to its length. The higher the value, the broader the pronotum. 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.	Attisano and Kilner 2015, Pessôa et al. 2017
Ratio **Back tibia length *to* Front tibia length** *Mean back:front tibia length*	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. Soil-digging tunnelers are expected to present a smaller ratio than dung-dwelling species. Rollers have more developed back tibias.	Hanski and Cambefort 1991, Inward et al. 2011
Ratio **Front tibia width *to* Front tibia length** *Mean width:length front tibia*	The width of the front tibia compared to its length. The higher the value, the broader and shorter the front tibia. 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.	Hanski and Cambefort 1991, Inward et al. 2011

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 (Fig. 1) is given in italics.

Trait-Based Metrics

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

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

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

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

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

Statistical Analyses

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

We performed all analyses in R (version 3.6.0, R Development Core Team 2020). We used the R script provided by Fontana et al. (2016) to compute TOP and TED, and the R package 'FD' (Laliberté and Legendre 2010; *dbFD* function) to compute FDis.

Results

We collected a total of 11,727 dung beetles belonging to 50 species (see Supplemental Material S5 [online only] for a full species list with abundances recorded in each GI patch, site, and study area). By comparison with previous inventories, our sampling design allowed us to have a good representation of the composition of local dung beetle communities in each study area (Supplemental Material S6 [online only]). The species composition in the two study areas was very different, with only four Aphodiinae species in common (*Aphodius cardinalis* Reitter, *Calamosternus granaries* L., *Colobopterus erraticus* L., and *Otophorus haemorrhoidalis* L.). Species richness was slightly higher in the steppe compared to the Alps (28 vs. 26), but the mean number of captured individuals in traps was seven times higher in the Alps (Mean ± SE: steppe = 48. 8 ± 4.0; Alps = 342. 3 ± 42.4).

Changes in Mean Trait Values in Response to Grazing Intensity

Mean trait values changed significantly between the GI patches and often similarly between the two study areas (Fig. 1). Both in the steppe and the Alps, dung beetles in LGI patches were, on average, larger than those in HGI patches (steppe [LGI > HGI]: $t = -9.02$, $P < 0.001$; Alps [LGI > HGI]: $t = -6.54$, $P < 0.001$;

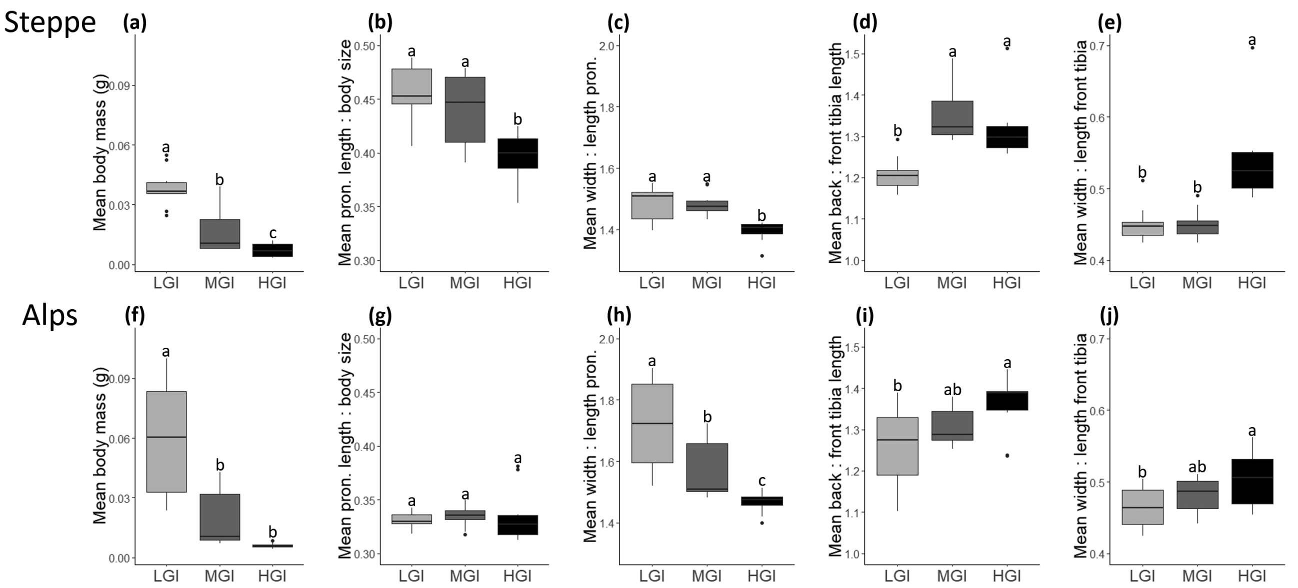

Fig. 1. Variation in the mean value of each trait used in the analyses (Table 2) between the GI patches in the steppe (top row) and the Alps (bottom row). For each response variable, three levels of grazing intensity (GI) were tested: Low (LGI), Moderate (MGI), and High (HGI). Differing letters (a, b, c) indicate significant differences between grazing intensity levels at α = 0.05 based on the standard linear models (refer to Supp Table 7.1 [online only] for statistical results of the pairwise comparisons).

Fig. 1a and f) and had broader pronotum (steppe [LGI > HGI]: $t = -5.19$, $P < 0.001$; Alps [LGI > HGI]: $t = -6.04$, $P < 0.001$; Fig. 1c and h). In the steppe, dung beetles had a larger-proportioned pronotum relative to their size in LGI and MGI patches ([LGI > HGI]: $t = -5.02$, $P < 0.001$; [MGI > HGI]: $t = -3.61$, $P < 0.001$; Fig. 1b), while no significant variation was found for this trait in communities in the Alps (Fig. 1g). Observed changes for leg-related traits in species assemblages were quite similar between the steppe and the Alps. Dung beetles in LGI patches had, on average, proportionately longer front tibias compared to back tibias (steppe [LGI < HGI]: $t = 4.03$, $P < 0.001$; Alps [LGI < HGI]: $t = 2.93$, $P = 0.01$; Fig. 1d and i) and narrower front tibias (steppe [LGI < HGI]: $t = 4.83$, $P < 0.001$; Alps [LGI < HGI]: $t = 2.75$, $P = 0.01$; Fig. 1e and j) compared to dominant beetles in HGI patches which had proportionately longer back tibias compared to the front tibias, and shorter, broader front tibias. Please refer to Supp Table 7.1 [online only] for statistical results for these comparisons, including estimates, df, t value and P value.

Changes in Trait Diversity in Response to Grazing Intensity

We observed some significant changes in trait diversity values between the GI patches (Fig. 2). In both the steppe and the Alps, trait richness (TOP) peaked in MGI patches (steppe [MGI > LGI]: $t = 2.84$, $P = 0.01$, steppe [MGI > HGI]: $t = -2.66$, $P = 0.01$; Alps [MGI > LGI]: $t = 3.00$, $P = 0.01$, Alps [MGI > HGI]: $t = -2.61$, $P = 0.01$; Fig. 2a and d). In the Alps, trait divergence (FDis) tends to be higher in species assemblages occurring in MGI patches [MGI > LGI]: $t = 2.05$, $P = 0.05$, [MGI > HGI]: $t = -2.81$, $P = 0.01$; Fig. 2e), while no significant trend was observed in the steppe (Fig. 2b). The results showed no significant trends in trait evenness (TED) between GI patches, both in the steppe and the Alps (Fig. 2c and f). Please refer to Supp Table 7.2 (online only) for statistical results for these comparisons, including estimates, df, t and P values.

Discussion

To date, only a few studies have addressed the responses of particular groups of arthropods to fine-scale heterogeneity in grazing intensity (e.g., Cole et al. 2010, Jerrentrup et al. 2014, Chillo et al. 2017). We found in this study that this scale of habitat patchiness matters for dung beetles. Because dung beetles are excellent fliers and actively forage for food by smell, they are able to move over long distances (Larsen and Forsyth 2005, da Silva and Hernández 2015), exceeding those separating the different GI patches within the sampled rangelands (Cultid-Medina et al. 2015). Despite this long-distance foraging, we demonstrated in both the steppe and the Alps that fine-scale variations in grazing intensity are likely to result in changes in morphological trait composition and in trait diversity of dung beetles communities, specifically in terms of trait richness and trait divergence.

How May the Spatially Heterogeneous Grazing Intensity Influence Dung Beetle Assemblages at a Fine Scale?

Response of Body Mass

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

First, body mass—or body size more generally—is a central parameter in animal life histories, as it interacts with most fitness-related traits (Peters 1983). A decrease in community mean body mass with increasing disturbance intensity has been demonstrated for several arthropod taxa (Simons et al. 2016, Wong et al. 2019). In dung beetles, differences in body size may be correlated with differences in behavior and fecundity, and such differences may explain the pattern observed for body mass, at least partially. Large dung beetles generally elaborate below ground nests in which the

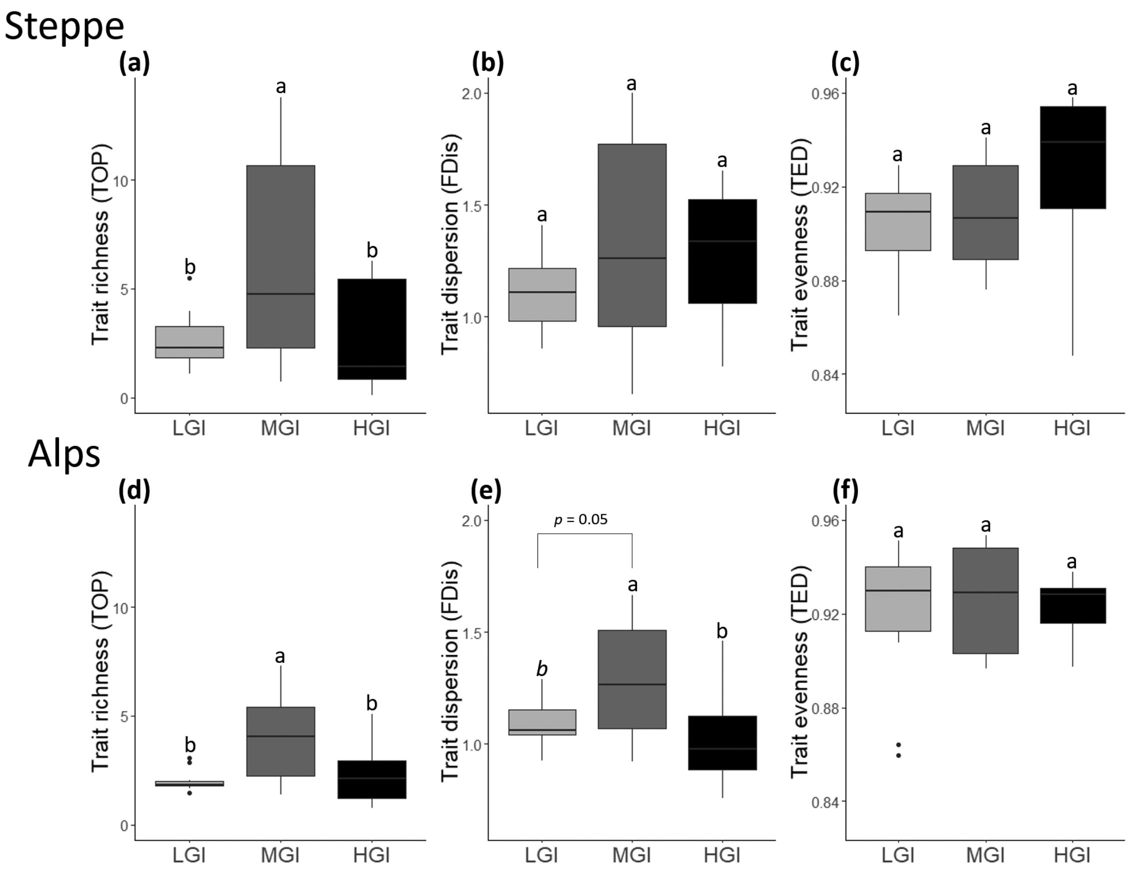

Fig. 2. Variation in trait richness (TOP), trait divergence (FDis), and trait evenness (TED) in species assemblages between the GI patches in the steppe (top row) and the Alps (bottom row). For each response variable, three levels of grazing intensity (GI) were tested: Low (LGI), Moderate (MGI), and 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 Supp Table 7.2 [online only] for statistical results of the pairwise comparisons).

offspring find food and shelter (Hanski and Cambefort 1991). This parental care compensates for the low fecundity of these species. To do their nest, adults of large species make numerous round trips between the ground and the surface to bury pieces of excrement; the entire nesting sequence may last from hours to several days (Klemperer 1979, 1982). One can hypothesize that repeated trampling of droppings in overgrazed areas might compromise the ability of these large species to make their nest efficiently. Smaller species (i.e., Aphodiinae species) that simply lay their eggs inside droppings or at the soil-dropping interface (Gittings and Giller 1997) should be less disturbed. However, larvae of these small species should be more sensitive to an intensive trampling of their living substrate on the surface (i.e., droppings) than those living belowground (i.e., larvae of burrowing beetles). Therefore, the large offspring production by small species may allow the persistence of individuals in overgrazed patches, contrary to large species—with few offspring—which are believed to be less adapted to highly disturbed habitats (Hanski and Cambefort 1991).

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

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

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

Response of Other Morphological Traits

Our results also support our hypothesis that morphological traits related to soil-nesting strategies are filtered out at the higher grazing intensity. Dung beetles occurring in lightly grazed patches tended to have relatively elongated and longer-proportioned front tibias compared to individuals at highly grazed patches, which had rather broad and shorter-proportioned front tibias. More developed front legs can be considered a morphological adaptation for building underground nests while broader legs can help dwellers to progress in the soft mass of dung (Beutel et al. 2013). Thus, the observed pattern in the steppe and the Alps is likely to reflect a decrease in soil-living individuals within assemblages in highly grazed patches. This result is in line with the findings of Jankielsohn et al. (2001) and Negro et al. (2011) in intensively grazed areas of the African Savannah and the Italian Alps, respectively. It was suggested that this pattern is accounted for by repeated trampling that disrupts the physical characteristics of soil, creating unfavorable conditions for species that oviposit (e.g., in tiger beetles, Cornelisse and Hafernik 2009) or build tunnels underground. In a recent study, Dabrowski et al. (2019) showed that South African dung beetles are able to dig and reproduce in highly compacted soils, but the effects of soil compaction may change depending on the species considered. However, presently little is known about the sensitivity of different European dung beetles to physically altered soil conditions. Measuring the soil hardness could have given us more information about this process; however, the very compact soil of the steppe prevented us to use the commonly applied tools (e.g., handheld penetrometer, Manning et al. 2016). We encourage future studies in explicitly exploring this link between soil physical disturbance due to trampling and the disappearance of soil digger dung beetles.

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

What are the Consequences of Those Processes for Trait Diversity?

The observed changes in morphological trait composition within dung beetle assemblages resulted in significant variations in some of the used multidimensional trait indices. In both the steppe and the Alps, dung beetle trait richness (TOP) is higher for species assemblages occurring in moderately grazed patches and decreased in the lightly and highly grazed ones. According to the theory of habitat filtering, environmental pressures are likely to filter organisms without suitable trait values to cope with local conditions (Cornwell et al. 2006, Pakeman 2011). This may result in reduced trait space, consisting of a restricted pool of the most adapted trait value combinations (Cornwell et al. 2006). In our study, specific morphological characteristics were selected at low and high grazing intensities. Specifically, as explained above, we suggest that livestock disturbance and high dropping density in intensively grazed patches selected mainly for small size and dweller species, while low disturbance intensity and resource availability in the lowest grazed patches selected for a restricted range of resource use strategies that enhance foraging efficiency. In moderately grazed patches, intermediate levels of resource availability and disturbance intensity (i.e., disturbance of soil characteristics) may create a wider range of potential niches, allowing the local coexistence of individuals with different ecological requirements. This, in turn, might increase the morphological trait space occupied by dung beetle communities, and therefore results in the observed higher trait richness in moderately grazed patches. This hypothesis is in line with the results of Jerrentrup et al. (2014) and Pöyry et al. (2006) for other arthropods groups (e.g., phytophagous insects), which had shown that species richness may peak at intermediate levels of sward height in temperate grasslands.

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

This result, however, was not observed for species assemblages in the steppe, where we did not observe the same significant differences in trait divergence. More specifically, and contrary to the observed pattern in the Alps, steppe dung beetle assemblages occurring in highly grazed patches did not show a significantly reduced trait divergence compared to those sampled in moderately grazed patches. This result may be due to different sampling conditions between the two steppe study sites. Indeed, the presence of a sheepfold in the 'Petit Carton' pasture (see Material and Methods—Study Areas and Sampling Design) prevented us from sampling directly in the resting area. As a consequence, at 'Petit Carton', the HGI patch was sampled in the surroundings of the sheepfold, and showed FDis values that were significantly higher than those observed for the HGI of the second steppe rangeland (i.e., 'Grosse du Couchant'; respectively FDis mean ± SE: 1. 52 ± 0.05 vs. 1. 03 ± 0.08; Mann–Whitney *U* test $P = 0.01$). It is likely that, contrary to our expectations (see Material and Methods—Study Areas and Sampling Design), grazing intensity in the sheepfold's surroundings was not as high as inside the outdoor resting place, with the result that the livestock-induced disturbance around the sheepfold was probably not strong enough to reduce trait divergence of the species assemblages, as was observed in other HGI patches.

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

Conclusions and Perspectives

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

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

Finally, using sets of morphological traits allowed us to comprehensively investigate the effects of environmental pressures, as they affect the multidimensional phenotype that reflects an organism's niche (Ricklefs and Travis 1980). However, for some taxa such as insects, the trait–environment relationship is still poorly understood. Moreover, many morphological features have multiple functional roles, and revealing how morphology differentially affects performance—or whether such a causal relationship even occurs—can be difficult (Moen 2019). We, therefore, strongly recommend further laboratory and controlled experiments to assess the functional relevance of eco-morphological traits of dung beetle communities. This is a fundamental step towards improving predictive trait-based studies with terrestrial arthropods.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

We thank the Biodiversity and Conservation Biology Research Unit of the WSL for their welcome. We are grateful to the staff at the Provence-Alpes-Côtes-d'Azur Conservatory of Natural Areas and the Vanoise National Park for their cooperation and assistance in this study. We thank the shepherds and sheep breeders for their cooperation. W.P. received a Ph.D. grant from University Paul Valéry Montpellier III, France, and a supplementary grant from the same university to work at the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) in Birmensdorf, Switzerland. S.F. was supported by the Swiss National Science Foundation, Project 315230_170200/1. The project also received financial support from the Vanoise National Park. All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. The capture and killing of insects (necessary to identify them) in the protected areas were allowed thanks to the specific authorization given for our scientific study.

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