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# Dung beetle community patterns in Western Europe: responses of Scarabaeinae to landscape and environmental filtering

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Otso Ovaskainen

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## Abstract

**Context** Mediterranean landscapes from Europe have undergone recent biodiversity changes. The intensification of human activities and the fragmentation of open habitats now affect many taxonomic groups, such as dung beetles, which have benefited from centuries of extensive herding. Nevertheless,

dung beetles' responses to landscape composition have been rarely investigated in this context.

**Objectives** We explored how dung beetle communities (species occurrences, abundances and traits) were influenced by temperature and by soil and landscape characteristics and examined residual co-occurrence patterns that may reflect interspecific interactions.

**Methods** We used an extensive dataset on Scarabaeinae dung beetles from southern France (31 species, 117 sites) to evaluate how landscape composition and fragmentation, climate and soil characteristics jointly influence dung beetle communities across this region. We used hierarchical joint species distribution models to characterize (co)variation in the responses of species and to connect such responses to species-specific traits.

**Results** Temperature, soil and landscape characteristics shape dung beetle communities and species' thermal tolerance was connected to their soil preferences. Fragmentation was negatively associated with beetle abundance while forest cover was positively associated with species richness and with abundance. There was little evidence of residual associations among dung beetle species, suggesting that species interactions do not play a major role in community assembly.

**Conclusion** K-selected species were over-represented among the rarest species. The effects of fragmentation and forest cover indicate that a conservation plan based on connected, heterogeneous habitats with low-density grazing should be promoted

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to preserve ecological functions linked to these insects.

**Keywords** HMSC · Landscape composition · Fragmentation · Mediterranean · Conservation

## Introduction

The transformation of ecosystems through anthropogenic land-use change is a major driver of biodiversity compositional change and loss (Sala et al. 2000; Cardinale et al. 2012; Newbold et al. 2015). Grasslands and other non-cultivated open habitats have undergone dramatic human-driven environmental changes affecting their specialized communities of plants and arthropods (Stefanescu et al. 2009; Miller et al. 2015; van Klink et al. 2015; Hilpold et al. 2018). In many parts of Europe, grazing and other traditional agricultural practices have been abandoned or intensified over the past century (Mazoyer and Roudart 2002; Poschlod and WallisDeVries 2002; Steinfeld et al. 2013), leading to grassland loss.

Landscapes around the Mediterranean and in southern European mountainous regions are no exception. In these areas, many localities have undergone intensification of human activities, fragmentation, dramatic losses in the extent of open habitats and declines in their constituent species, especially since the twentieth century (Sirami et al. 2010; Dengler et al. 2014). These ecosystems have their origins in the gradual anthropogenic clearing of a primeval landscape comprising steppes and forest massifs that were initiated in the Neolithic, lasted until the Iron Age, and resumed in the Middle Ages (de Keroualin 2003; Sirami et al. 2010). However, the advent of the agricultural revolution in the 1950s, the subsequent rural exodus and shift towards other types of agriculture (e.g., increasing dominance of viticulture in the plains) and energy consumption (from wood to fossil), resulted in the gradual abandonment of herding and traditional agriculture and in the expansion of woodlands and forests into formerly open habitats. In lowlands and hills, the intensification and specialization of agricultural practices and the decline in the area and number of grassland patches endanger the specialized communities of plants and arthropods in these habitats (Stefanescu et al. 2009; Miller et al. 2015; van Klink et al. 2015; Hilpold et al. 2018).

Mountainous regions have, in contrast, experienced different trends in grassland cover since the end of the twentieth century, as herd sizes have remained more constant (or even increased) in some areas (e.g., in the southern-French Alps, Garde et al. 2014). For the last 20 years, European policies have substantially supported livestock-breeding practices as a management tool for grasslands in order to preserve their biodiversity and ecosystem services (Nori and Gemini 2011; Lostrangio and Clotteau 2021).

In fragmented landscapes, the local persistence of species in remnant favorable habitat patches may depend not only on local habitat structure and available resources, but also on processes operating in the wider landscape or regional land mosaic (Saunders et al. 1991; Bennett et al. 2004). Broad-scale parameters of importance include the total area of favorable habitat and its level of fragmentation within landscapes (Bennett et al. 2004; Rösch et al. 2013). From a conservation perspective, the importance of adopting a landscape to regional perspective on land-use change in rural environments is well recognized, and several regional-scale conservation strategies have been established (Bennett et al. 2004; Santiago-Ramos and Fera-Toribio 2021).

In temperate regions, grasslands constitute an important ecosystem for various insect communities. In south-temperate regions, grassland insects have experienced large declines in areas where agro-pastoral practices have declined or agriculture has intensified (Sánchez-Bayo and Wyckhuys 2019). It has been shown that low dispersal abilities but also high ecological specialization may explain the sensitivity of some insect groups to grassland fragmentation (Tscharntke et al. 2002). Many European Scarabaeinae dung beetles (Coleoptera: Scarabaeidae), most of which specialize in consuming and reproducing from the feces of herbivorous mammals, fall into this category. In Western European countries, these insects benefited from agro-pastoral practices for thousands of years (Buse et al. 2015). However, the progressive local abandonment of these practices has led to changes in dung beetle communities, including shifts in community structure and diversity, decreasing individual abundances and the loss of some *K*-strategist species (Lobo 2001; Carpaneto et al. 2007; Tocco et al. 2013; Tonelli et al. 2017; Cuesta and Lobo 2019; Numa et al. 2020). Around the Mediterranean, dung resources provided by wild ungulates

in reforested landscapes are insufficient to ensure the maintenance of species diversity (Jay-Robert et al. 2008a). On the other hand, the intensification of agricultural practices also appears to be detrimental for dung beetle communities (Hutton and Giller 2003).

In Europe, dung beetles' responses to landscape composition and configuration have been rarely investigated (Numa et al. 2009, 2012; Verdú et al. 2011). However, in south-temperate regions, given the regional declines observed in some countries (Lobo 2001; Carpaneto et al. 2007) and the recent dynamic to establish the global conservation status of this group (Numa et al. 2020), a landscape perspective is necessary to adjust regional conservation policies and thereby mitigate the observed declines.

To investigate communities' responses to land use processes, we should account for multiple other sources of variation in species distributions as well. Communities in local patches are assembled from larger regional species pools, shaped by biogeographical history and niche-related processes operating over regional extents (Ricklefs 1987; Cornell and Harrison 2014). Within patches, local environmental conditions and biotic interactions influence co-occurrence patterns (Wiszniewski et al. 2013; Kraft et al. 2014). Across scales, species-specific characteristics, i.e., functional traits (Violle et al. 2007), modulate interspecific interactions, the propensity of species to reach and colonize habitat patches, and to secure resources and reproduce in those habitats. Recent statistical advances include new hierarchical joint species distribution models that allow variation and covariation in the responses of individual species to the characteristics of their environment to be evaluated, and such responses to be connected to species' traits (Ovaskainen et al. 2017). The use of these models has proven informative in assessing the effects of land use on species communities (e.g., Rocha et al. 2018).

In the present study, we evaluate how landscape composition and fragmentation may influence West-European dung beetle communities over regional extents. To answer this question, we employ an extensive dataset on Scarabaeinae dung beetles collected from southern France, extending from lowland Mediterranean environments to the Alps and Pyrenees, a region characterized by a complex topography which triggers strong gradients in habitat structure (vegetation, soil, etc.), climate and human land use, resulting

in a high regional species richness of Scarabaeinae (Lobo et al. 2002; Lumaret et al. 2008; Jay-Robert et al. 2008b). In this area, pastoral activity that maintains high levels of dung beetle species diversity (Jay-Robert et al. 2008a; Errouissi and Jay-Robert 2019) has been declining for decades.

We hypothesize that, like other exothermic insects, dung beetles' occurrences and abundances might be influenced by abiotic filters, notably temperature. Also, as all Scarabaeinae species dig tunnels where the larval development takes place, the soil matrix should also be an important determinant of species presence. Furthermore, we hypothesize that habitat fragmentation may influence the Scarabaeinae community by filtering species according to their traits, such as body size and nesting behavior. We ask how dung beetle distributions are shaped by these factors and examine residual co-occurrence patterns not explained by environmental factors, which may reflect interspecific interactions among taxa. Specifically:

1. How do soil, climate and landscape structure define dung beetle species distributions and community composition?
2. Which traits mediate the responses of dung beetle species to environmental conditions?
3. Are there positive or negative species associations that are unexplained by environmental conditions, possibly reflecting biotic interactions among dung beetle species, or alternatively their responses to some environmental predictors not included in our model.

## Materials and methods

### Data sampling and site characteristics

Fieldwork was conducted from 2013 to 2021 in southern France, during the peak activity period of Scarabaeinae dung beetles within the surveyed biogeographic regions: in April–May in the lowland Mediterranean habitats and in June–July in the mountainous regions (Pyrénées, Alps and Cévennes). Sample sites (N = 116) were mostly open (grasslands and garrigue) and ranged from 0 to 2483 m in elevation. For each field session, the number of traps used (1–20, with a mean of 4 traps per site) and the time span over which these were in the field was recorded

(range 24–72 h) to quantify sampling effort. Lobo et al. (1998) showed that 2 traps can be enough in Mediterranean lowlands to obtain 85% of total dung beetle abundances and 80% of the biomass. Trapping efficiency is expected to be higher still in mountains, where communities are dominated by a low number of species (Jay-Robert et al. 2008a; Tocco et al. 2013; Tonelli et al. 2018). Detail on the effort and dung beetle abundances for each site are available in Appendix 1.

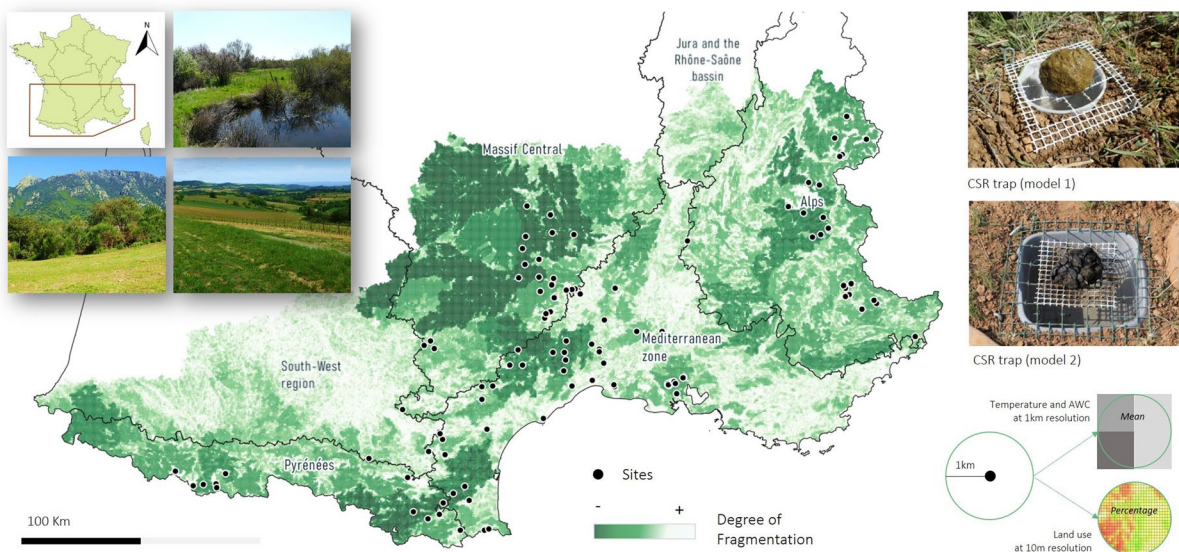
Insects were collected using dung-baited pit-fall traps as described in Lobo et al. (1998; CSR traps). Specifically, we used buried plastic basins (trap designs 1 and 2; Fig. 1) filled with soapy water which were topped with a grid in which we deposited 200–300 g of bovine and/or ovine dung. Attracted by the bait, the insects slip through the grid, fall into the bowl and drown. Although some dung beetle species may have certain trophic preferences or be attracted to dung from different origins (omnivores, ruminants, monogastric herbivores, etc.), most have a large trophic spectrum (Martín-Piera and Lobo 1996; Dormont et al. 2007; Wurmitzer et al. 2017). In the Western Palearctic, it has been shown that cow and sheep

are equally the most attractive baits (Dormont et al. 2007). This sampling method allows abundance data to be collected.

#### Statistical framework and data selection for analyses

The complete dataset consisted of the abundances of 31 dung beetle species (Scarabaeinae) collected at 117 sample sites (Fig. 1). We analyzed the data with a Hierarchical Model of Species Communities (HMSC; Ovaskainen et al. 2017; Ovaskainen and Abrego 2020), a joint species distribution model (Warton et al. 2015). As HMSC species-level analyses are not informative for species with very sparse data, we included only those 21 species that had at least ten occurrences across samples in the models.

The response variable was a vector of the abundance of each species across the samples. Due to the zero-inflated nature of the data, we fitted a hurdle model, i.e. one model for presence-absence data (probit regression), and another model for abundance conditional on presence (a linear regression of the log-transformed count data, with absences masked as missing data).



**Fig. 1** Sample site locations in Southern France, and some photo illustration of the diversity of the sites, plotted on a map representing the degree of fragmentation of favorable dung beetle habitats (meadows, grasslands and moors) (Corine land cover data) by urban areas, roads and forest patches. Darker green shades indicate less fragmented dung beetle habitats and

paler shades indicate more fragmented habitats. On the right are photographs of the two CSR trap designs used during sampling sessions (model 1: 15 cm in diameter, model 2: 20 cm on each side). At the bottom right corner we illustrated also how the abiotic variables were calculated at 1 km<sup>2</sup> scale

## Fixed and random effects

In order to understand how dung beetle species respond to landscape and environmental filtering we included as model fixed effects the following environmental variables: (1) the second order polynomial of mean annual temperature (Bio 1 from the Chelsa dataset, period 1980–2010s; Karger et al. 2017, 2018), (2) the predicted available water capacity for the topsoil fine earth fraction (AWC) derived from topsoil physical properties (texture) for Europe (Ballabio et al. 2016; European Soil Data Centre), (3) the percentage of favorable open habitat and (4) the percentage of forest habitat (open and forest habitat OCS categories from the value-added data processed by CNES for the Theia data center [www.theia-land.fr](http://www.theia-land.fr) using Copernicus products, year 2018), and (5) fragmentation of favorable habitat (meadows, grasslands and moors) by urban and forest patches (OCS habitat categories), calculated with GRASS software (GRASS Development Team 2020) using the “cross-boundary connections” approach (Moser et al. 2007). Other candidate variables such as precipitation and percentage of urban land use were withdrawn after a correlogram showed high correlations ( $R > 0.6$ ) and therefore not used in the models; similarly, soil pH was preferred over AWC, as AWC is not only correlated to sand-clay-silt percentages and therefore is a stable soil property over time, while pH shows a more rapid reaction, potentially introducing bias into the analysis.

The landscape structural variables (3, 4 and 5) were characterized at a spatial resolution of 1 km<sup>2</sup> buffer around the study site, respecting the

resolution of 1 km<sup>2</sup> of variables (1) and (2). We also included log-transformed sampling effort (the number of traps used multiplied by the duration that they were installed in the field) as a fixed effect in order to account for this potential bias.

As random effects, we included sampling year and a spatially explicit random effect based on the sample site coordinates. As sample sites were scattered among four different bioregions (Mediterranean, Pyrenees, Central Massif, Alps), we added the identity of the bioregion as another random effect in the model.

## Species traits

Species traits can be used as predictors in HMSC to model the expected responses of species to the environmental covariates. We included three traits as proxies for relevant biological mechanisms (“soft traits” in the sense of Lavorel and Garnier 2002) that are expected to influence dung beetle responses to land-use, soil and climatic gradients: species’ body length, temperature range tolerance and tunnel architecture (Table 1).

Body size is a central parameter in animal life histories, as it interacts with most fitness-related traits (Peters 1983). In Scarabaeinae dung beetles, this feature can be related to: (i) nutritional needs (larger species need sufficient resource for nesting, thus depending on high levels of dung availability in their environment, Nichols et al. 2013), (ii) thermal requirements (in the studied region, larger Scarabaeinae are mostly distributed in warm habitats; Lumaret and Kirk 1991), and (iii) resource acquisition (larger species are often considered to be more efficient in

**Table 1** Description of species’ traits selected: trait type (continuous or categorical), biological relevance (examples of mechanisms for which each trait is a presumed proxy) and sources of trait data

Trait	Trait type	Biological relevance	Source
Mean body length (mm)	Continuous	Nutritional needs Reproductive rate Dispersal capacity	Paulian and Barraud (1982), Lumaret (1990)
Temperature range tolerance (°C)	Continuous	Thermal requirements	Based on the ScaraB’Obs data base with more than 40,000 dung beetle observations across France. Calculated with Qgis and based on data from Karger et al. (2017, 2018)
Tunnel architecture	Categorical (two categories: “simple” nest or “ramified” tunnels)	Reproductive rate	Simplified from Halffter and Edmonds (1982)

dung exploitation, Doube 1990; Perrin et al. 2021). In southern Europe, studies have previously found that body size can mediate dung beetles' responses to various environmental variables. For example, this trait may determine the sensitivity of species to variation in resource (i.e., dung) quantity under contrasting grazing conditions (Perrin et al. 2021; Tonelli et al. 2017) and explain patterns of community reshuffling under historical changes in vegetation cover and climate (Cuesta and Lobo 2019). Here we used log-transformed mean body length (mm) retrieved from the literature on French dung beetle species (Paulian and Baraud 1982; Lumaret 1990).

The observed temperature range of the species in France was used as a proxy of the thermal niche of each Scarabaeinae species. Temperature tolerance influences the range of thermal conditions under which species can live (Sunday et al. 2012, 2014). We expected that temperature tolerance might influence species responses to landscape structure (e.g., via the effects of vegetation structure on microclimatic conditions; Giménez Gómez et al. 2020), elevation and other climatic gradients structuring the studied region (Lobo et al. 2002; Jay-Robert et al. 2008a). Because temperature tolerance may also be linked to desiccation tolerance, one can hypothesize that this trait also influences the sensitivity of species to microclimatic soil conditions that are linked to soil characteristics (Nervo et al. 2021a, b). This variable was calculated for each species by using the Scarab'Obs dataset of dung beetle observations on the French territory (40,000 observations; <https://scarab-obs.fr/>) and by excluding the 1st and 10th quantile, thus having a reliable min and max. The presence observations were projected onto a long-term annual mean temperature map (Chelsa bioclim variable Bio1; Karger et al. 2017, 2018) to retrieve the temperature values at each known observation site. We then calculated the quartiles of the extracted mean temperature values for each species, then subtracted the lower from the upper quartile value, to gain the interquartile range, which we used as a proxy for species' temperature tolerance.

Tunnel architecture was defined as a proxy of nesting behavior, and particularly of the level of parental care (Halffter and Edmonds 1982). This categorical information was simplified into two levels: ramified tunnels, which are the most common tunnel architecture among the studied taxa (typical nest architecture

for species belonging to the tribes of *Onthophagini*, *Oniticellini* and *Onitini*), and simple ones, typical of species from *Scarabaeus*, *Gymnopleurus*, *Sisyphus* and *Copris* genera. Typically, species building ramified tunnels have more progeny than species building simple nests, whereas the latter compensate for their lower reproductive rates with a higher level of parental care (Halffter et Edmonds 1982). The literature on insect responses to disturbances and land use changes indicates that species with lower reproductive rates can be disadvantaged (due to their smaller population sizes), whereas small species with fast life histories can recover rapidly after disturbance (Ribera et al. 2001; Simons et al. 2016; Koltz et al. 2018). Information about species' tunnel architecture was retrieved from the functional classification of Scarabaeinae dung beetles established by Doube (1990), supplemented by data from other sources for species that were not included in this classification (Klemperer 1981; Halffter and Edmonds 1982).

#### Model fitting

We fitted the model with the R-package HMSC (Tikhonov et al. 2020) assuming the default prior distributions. We sampled the posterior distribution with four Markov Chain Monte Carlo (MCMC) chains, each of which was run for 375,000 iterations, of which the first 125,000 were removed as burn-in. The iterations were thinned by 1000 to yield 250 posterior samples per chain, giving 1000 posterior samples in total. To assess MCMC convergence, we examined the distribution of the potential scale reduction factors over the fixed and random effect parameters (equivalent to the Gelman-Rubin statistic, Gelman et al. 2013).

#### Model performance and predictions

We examined the explanatory and predictive powers of the probit models through species-specific Tjur  $R^2$  and AUC, which measure how well the model discriminates those cells at which the taxon occurs from those in which it does not occur. The explanatory and predictive powers of the abundance models were measured by  $R^2$ . To compute explanatory power, we calculated model predictions based on models fitted to all the data. To compute predictive power, we performed a fivefold cross validation, in which the sampling units were assigned randomly to fivefolds, and

predictions for each fold were based on a model fitted to data on the remaining four folds.

To address our first hypothesis, we ran variation partitioning to quantify the percentage of total variance in species occurrences vs. abundances explained by each environmental covariate. We also plotted the species' predicted occurrence and abundance responses to each environmental covariate (i.e., their  $\beta$  parameter values, highlighting those positive or negative responses for which there was strong posterior support at  $P > 0.95$ ), and continuous predictions of dung beetle species richness and total abundance as a function of each covariate.

To address our second hypothesis, we estimated the proportions of variance in species occurrences and abundances that could be explained by the three selected ecological traits. By examining the gamma ( $\Gamma$ ) parameters of the models, we furthermore assessed whether there was strong posterior support ( $P > 0.95$ ) for positive or negative relationships between species' predicted responses to each environmental covariate (i.e., their  $\beta$  values) and their trait values, for each of the three traits separately.

Finally, HMSC provides estimates of residual pairwise associations among species, i.e., of associations that remain after controlling for species' environmental responses. We visually explored these associations to address hypothesis 3, regarding potential biotic interactions among dung beetles.

## Results

### Model performance

Explanatory power for both the species occurrence and abundance (conditional on presence) models was good. For the occurrence models, mean Tjur  $R^2$  was 0.46 (range 0.29–0.67) and mean AUC was 0.94 (range 0.86–1.00); for the abundance models mean  $R^2$  was 0.42 (range 0.16–0.77). Predictive performance was also reasonably good for the occurrence models, with mean cross-validated Tjur  $R^2 = 0.34$  (range 0.19–0.57) and mean cross-validated AUC = 0.86 (range 0.74–0.97). However, for the abundance models, predictive performance was relatively high (cross-validated  $R^2 > 0.4$ ) for just two of the 21 species, *Onthophagus vacca* and *Copris hispanus*, but was negligible for 12 out of the 21 species

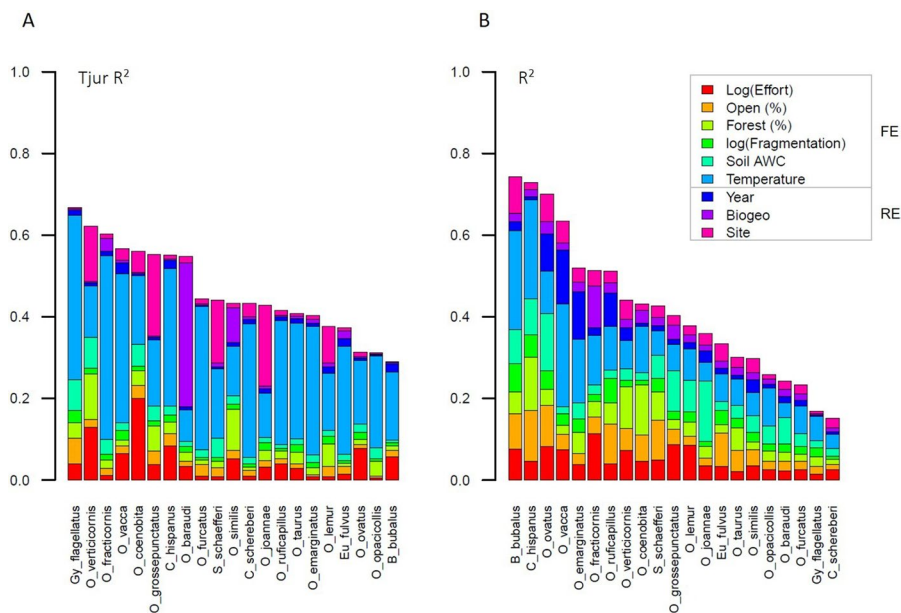
(cross-validated  $R^2 < 0.05$ ) (supplementary material). Therefore, the abundance model results should in many cases be interpreted with caution. High uncertainty in the abundance predictions may reflect the fact that most of the sites were visited just once at the activity peak of the community and that the models did not include any information about the presence of livestock nearby, and hence poorly reflect dung beetle population dynamics and its drivers.

### Climate, soils and landscape structure as drivers of dung beetle community structure

Mean annual temperature contributed most, on average, to explained variation in dung beetle occurrences (Fig. 2A). For 81% of species (17 out of 21), there was support for a relationship between temperature and occurrence (Fig. 3A), which was positive for most species and hump-shaped for three species (supplementary material). In contrast, sampling year explained only a minor component of variation, indicating that species occurrences and abundances did not differ markedly among years. Landscape variables played a secondary role to climate, explaining on average 7% of variation" (i.e., sum of variation explained by open %, forest% and fragmentation, averaged across species = 7%) (Fig. 2A) and, where detected, their effects were positive (Fig. 3A). Soil AWC also played a minor role. For four species, the spatial random effect explained as much variation as temperature, implying that the models failed to include all relevant drivers of their occurrence distributions, and for one species (the alpine endemic *O. baraudi*) biogeographic region was the main explanatory variable. For approximately 40% of species, occurrence was positively associated with sampling effort with at least 95% posterior probability (Fig. 3A) and, for 25% of species, sampling effort substantially explained their occurrence distributions, which may indicate that these species are either less frequent, or more variable in their spatiotemporal distribution, or are less easy to detect than other species with dung-baited traps.

When species abundances within occupied sites were modelled (Figs. 2b, 3b), mean annual temperature explained a smaller fraction of variation than in the occurrence models, and its contribution was more similar to or even exceeded by that of the land cover parameters (Fig. 2b). Abundance responses to mean





**Fig. 2** Variation in **A** dung beetle species occurrences and **B** abundances conditional on their presence partitioned into fractions explained by six fixed and three random covariates. The fixed effects (FE) are log-transformed sampling effort and five environmental characteristics of the sample sites (annual mean air temperature, soil AWC, the percentages of open vs. forested habitat and a log-transformed index of fragmentation

in the surroundings of the sample site and). The three community-level random effects (RE) are sampling year, biogeographical region and the spatial random effect of the site. Species are ordered from left to right according to the total amount of variance explained by these covariates (bar height). Total explained variation (bar height) is quantified as  $Tjur R^2$  in the occurrence models and  $R^2$  in the abundance models

annual temperature were furthermore not detected (with strong support) for any individual species. However, we found evidence that land cover and soil AWC, in particular, structure the abundance distributions of some dung beetle species.

Mean annual temperature was predicted to have a positive relationship with dung beetle species richness (Fig. 4A). Species numbers were also predicted to increase with increasing forest cover, as well as with sampling effort. Individual abundance at occupied sites was predicted to be structured by all the covariates except for mean annual temperature (Fig. 4B). Dung beetle abundance was predicted to increase as a function of sampling effort, both open and forested habitat cover and soil AWC, and to decline as a function of fragmentation.

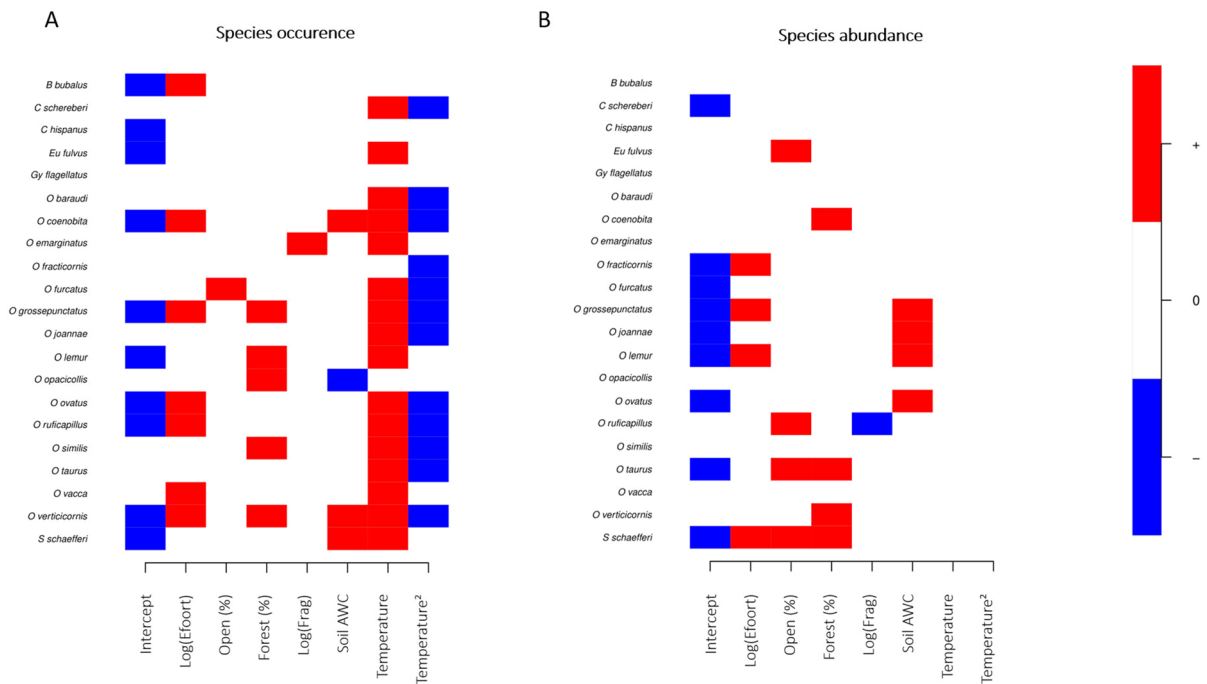
#### Dung beetle traits and environmental responses

The three selected ecological traits (species' temperature tolerance, body size and tunnel architecture) together explained 70% of overall variation in the

occurrence distributions of dung beetles, and 60% of their abundance variation across occupied sites. The predicted responses of dung beetles to the environmental covariates did not, however, vary consistently as a function of specific traits, except in one case. There was strong posterior support ( $P > 0.95$ ) for a positive relationship between species' observed temperature ranges across France and their predicted 'niche positions' (beta parameter values) on the soil AWC gradient, when these were calculated based on occurrence data. Specifically, species typical of soils with relatively high-water holding capacities had broader temperature tolerances than species of more droughty soils.

#### Biotic interactions among dung beetles?

There was limited evidence of residual associations among dung beetle species at any level of the sampling hierarchy (bioregions, sample sites or among years). This implies that most of the covariance in their observed occurrence and abundance



**Fig. 3** Dung beetle species' predicted **A** occurrence and **B** abundance responses to sampling effort and six environmental covariates (the percentages of open vs. forested habitat and a log-transformed index of fragmentation in the surroundings of the sample site, soil AWC, annual mean air temperature and

its square term). Positive (red) vs. negative (blue) responses per species and covariate are illustrated. These represent the  $\beta$  parameter values that were estimated to be positive or negative with at least 95% posterior probability

distributions was driven by species' habitat preferences, and that this was successfully captured by the environmental covariates in the models.

In the occurrence models, there were positive residual correlations among a small subset of species at the site level. We found no evidence of negative interspecific associations. In the species abundance models, positive residual correlations were observed between sampling years for a few species, but there were none at the levels of either site or biogeographical region.

At the level of biogeographical region, some structure in species occurrences distributions that was unexplained by either the temperature gradient or other covariates was furthermore detected.

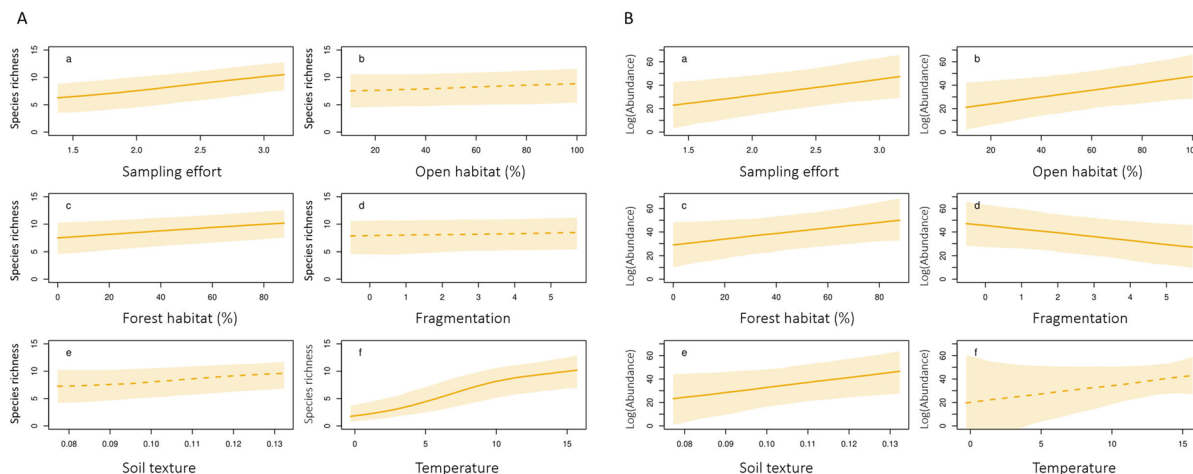
Spatial autocorrelation was detected with strong posterior support in both the species occurrence and abundance models up to typical scales of 29 and 102 km, respectively. This may however reflect spatial bias in the sampling scheme due to the fact that some of the sampling was specifically conducted in

protected areas in the mountainous French National Parks.

## Discussion

### Diversity patterns response to environmental characteristics

Patterns of dung beetle occurrence in southern France are strongly structured by regional variation in climatic conditions. In the introduction we mentioned the importance of grazing in shaping Mediterranean and Alpine landscapes since the Neolithic era (Sirami et al. 2010; Dengler et al. 2014). We can add to this the fact that southern-Palaearctic communities were heavily shaped by the last glaciation, as this area acted as a refuge for many taxa during the Pleistocene, allowing the maintenance of thermophilous species, including many insects (Balleto and Casale 1991; Lumaret and Kirk 1991). It is not therefore



**Fig. 4** **A** Predicted species richness of dung beetles as a function of (a) sampling effort and five environmental covariates (the percentages of (b) open vs. (c) forested habitat, (d) a log-transformed index of fragmentation, (e) soil AWC, and (f) annual mean air temperature). **B** Predicted abundance of dung beetles as a function of (a) sampling effort and five environmental covariates (the percentages of (b) open vs. (c) forested habitat, (d) a log-transformed index of fragmentation, (e)

soil AWC, and (f) annual mean air temperature). The shaded areas represent the 95% credible intervals and lines represent the predicted median abundance. Dashed lines represent cases where a directional trend in species richness and abundance along the gradient in question was not supported with at least 95% posterior probability. These are marginal predictions, where values for all covariates apart from the focal gradient are fixed at their mean value in the dataset

surprising to see that, for dung beetles, mean annual temperature is a major predictor of present-day species distributions. Lobo et al. (2002) similarly found a positive correlation between temperature and species richness in French Scarabaeinae dung beetles. A good example of a species whose presence is clearly structured by climatic conditions is *E. fulvus*, a thermophilous species with a narrow temperature range, the occurrences of which were positively correlated with temperature. Species abundances are also strongly modulated by landscape composition (captured here by land cover variables) and by the ability of the soil to retain water. On average, just over 30% of variance in both species occurrences and abundances was explained by the chosen environmental variables, but environmentally explained variance was close to 60% for a few species.

Various stochastic processes, including dispersal, environmental stochasticity and ecological drift may have contributed to residual (unexplained) variance in our models (Ovaskainen et al. 2017). We were unable to directly include any dispersal traits, as these are poorly known for dung beetles (Roslin 2000). Environmental stochasticity may also have been high, because sites were usually visited only once and were

not homogeneously documented. Furthermore, some unexplained variance in our models could be related to dung beetles' foraging dynamics. Although we know that there is pastoral activity in some areas (i.e., in study sites in the Alps), for other sites we lacked this information (i.e., sites near the cities of Montpellier and Perpignan), and hence we could not include information on livestock presence in our models. Available food resources for dung beetles furthermore reflect not just the presence or absence of grazing but also its modalities—e.g. grazing pressure (Perrin et al. 2020, 2021) and historicity (Buse et al. 2015). Additionally, there is evidence that fine-scale variations in microclimatic conditions that are linked with grazing intensity also structure dung beetle communities at a local scale (Jay-Robert et al. 2008a). Unfortunately, it was not possible to obtain reliable data on livestock activities systematically over many sites. As our study focused on variables at a scale of 1 km<sup>2</sup> around the sample sites, we may have failed to account for some environmental structure relevant for dung beetle distributions at the micro- or meso-scale, such as vegetation composition and configuration (Verdú et al. 2011; Numa et al. 2012).

Nonetheless, our models showed support for both positive and negative effects of several environmental covariates on community patterns (species richness, total abundance). While species richness was predicted to increase with increasing mean temperature and sampling effort, our results suggest that forest cover also promotes species richness, which was somewhat unexpected. Although all our sample sites were placed in open habitats, the presence of forest within the 1 km<sup>2</sup> area around the sites may augment habitat structural heterogeneity, which is known to be favorable for species coexistence (Jay-Robert et al. 2008b). A few species (e.g., *Onthophagus coenobita*, *O. verticicornis* and *Sisyphus schaefferi*) are furthermore commonly encountered in grazed woodlands, sometimes at high abundance (Errouissi and Jay-Robert 2019), which is in line with our results (Fig. 2). Moreover, species abundance increased with sampling effort, soil AWC and the percentages of both forest and open habitats. Fragmentation, in contrast, was negatively associated with total dung beetle abundance. Thus, although there was limited evidence that fragmentation affects the abundance of individual species (e.g., *O. ruficapillus*), its overall impact on dung beetle communities is negative, underlining the role of habitat connectivity for population dynamics (Zhang et al. 2017). The positive role played by both open and forest habitats on insect abundance here implies that dung resources were available in both habitats. This may reflect traditionally extensive grazing in the Mediterranean region, where herds and flocks traverse these different habitats (Blondel and Aronson 1999). The positive role played by soil AWC in our models may reflect its importance for the endogenous larval development of Scarabaeinae species. Soils with a high-water availability are typically also well oxygenated, which is important for larval development in organic matter where they undergo diverse interactions with microorganisms. Dry soils (e.g. sandy soils) may also impede the development of larvae in species that are especially sensitive to desiccation. In southern France, the consistent responses of Scarabaeinae to environmental variables, and particularly to the temperature gradient, that we observed are also supported by earlier findings (Lobo et al. 2002; Dortel et al. 2013; Hertzog et al. 2014) and are consistent with the African origin of the group (Cambefort 1991; Breeschoten et al. 2016).

Our results showed that fragmentation of favorable open habitats was associated with lower total beetle abundances. However, this process seems to not affect the communities' species richness, which is somewhat surprising as, for example, larger species are usually particularly sensitive to habitat destruction or fragmentation (Lobo 2001; Tonelli et al. 2018). It is, however, important to note that one third of the sampled species (10/31) was too rare to be modeled, and that these included many of the largest *K*-selected species (e.g., species in the genera *Scarabaeus*, *Copris* and *Bubas*); hence our capacity to detect the effects of landscape disturbances on species richness was significantly impeded. Overall, we suspect that the relationship that we observed between the Scarabaeinae community and anthropogenic habitat fragmentation signals an ongoing negative trend that does not bode well for the future. Among the species studied, we did not find evidence that traits, like body size, were linked to species-sorting along environmental gradients, except for a positive relationship between species' temperature distributional range in France and their local scale habitat preferences in terms of soil moisture. But once again, this might be linked to the bias mentioned above.

Competition as a structuring force in dung beetle communities has been demonstrated in earlier studies (Finn and Gittings 2003) and both temporal and successional niche partitioning in temperate dung beetles are thought to facilitate their coexistence, and therefore their co-occurrence (Sullivan et al. 2017a, b). Nonetheless, residual patterns of species co-occurrence (i.e., associations that were unexplained by the modeled environmental variables) were relatively rare in our dataset, and those residual associations that we did observe were mostly positive. Positive residual associations between *S. schaefferi*, *Caccobius schreberi* and five *Onthophagus* species are likely to reflect their shared habitat preferences, i.e., Mediterranean shrublands with pastoral activity. At a biogeographical scale, two typical species of high-altitude alpine grasslands (*O. baraudi* and *O. fracticornis*) showed negative residual associations with *O. similis*, another mountain species abundant in the Massif Central and the Pyrenees. We did not detect any evidence of negative residual associations between species at finer scales. However, this may simply reflect the spatial, temporal and taxonomic limitations of our sampling scheme. Both species co-occurrence patterns and

environmental associations are scale-dependent and vary in time. Thus, the scales at which species and environmental parameters are sampled are likely to influence the apparent importance of abiotic factors vs. biotic interactions like competition as drivers of community structure (Stephens et al. 2020). Abundance patterns are likely to have been biased by the fact that most sites were visited just once. Consequently, we may have missed the phenological peak of species co-occurrences. Our trapping methods furthermore aggregate species observations over time, and hence do not allow possible avoidance behaviors in resource and habitat use to be observed.

### Dung beetles, pastoral practices and conservation

First, the strong effect of annual temperature on species richness underlines the peculiarity of the study region, which is a transition zone in which most species are restricted to the Mediterranean lowlands. Second, our findings are connected with both current cattle breeding and management practices and conservation policies implemented in southern France. We infer that the ongoing fragmentation of open habitats poses a risk to Scarabaeinae communities, particularly in terms of individual abundances, and possibly to their ecological functions. Due to huge increases in urbanization within this biodiversity hotspot (DREAL LR 2015), conservation issues are of key importance. Agri-Environmental-Climate Schemes, conservation measures funded by European Union, are designed to sustain farming models that augment or maintain biodiversity in areas that are subject to the loss of open habitats (Kleijn and Sutherland 2003; Batáry et al. 2015; Calvet et al. 2019). Maintaining open habitats is therefore one of the priorities of the French National strategy for protected areas (Ministère de la Transition écologique and Ministère de la mer 2021).

However, the current trend of increasing livestock densities within small areas in Europe may also pose a threat to Scarabaeinae species (Hutton and Giller 2003). A similar conclusion (i.e., losses of specialist species with increasing intensification of cattle and sheep-farming) was reached for butterflies, both at a French and at a European scale (Van Swaay et al. 2016; Louboutin et al. 2019). Intensified cattle breeding is often associated with an increased use of parasiticides, which constitutes a further risk factor for dung beetles and consequently alters ecological

functions in pasturelands (Manning et al. 2017; Verdú et al. 2018).

### Conclusion

Our study of Scarabaeinae dung beetle communities showed that temperature gradients strongly structure species occurrence distributions in southern France, while soil and landscape variables are more important for species abundances. The high proportion of rare species in this region likely reflects the magnitude of Scarabaeinae declines in southern Europe since the mid-twentieth century. The negative relationship that we observed between the fragmentation of favorable habitats and total abundance leads us to suspect that dung beetle population declines are still ongoing. Current patterns of occurrence and abundance of Scarabaeinae species in the study area are likely to partially reflect past conditions. To preserve ecological functions that are beneficial to Alpine and Mediterranean socio-ecosystems in the long run, we should plan and propose new grazing management strategies now.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

### Declarations

**Competing interests** The authors declare no competing interests.

**Ethical approval** NA.

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