



Sheep and cattle grazing regimes differentially affect ground beetle and ant communities in Mediterranean cork oak woodlands

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Abstract

1. Grazing has a substantial impact on European grasslands, with both intensification and abandonment posing threats to biodiversity and ecosystem services. Sustainable agroforestry systems integrating grazing, agriculture and conservation offer a multifunctional solution to maintain productivity, biodiversity, cultural heritage and mitigate land degradation.
2. In this study, the impact of grazing on Mediterranean woodlands, characterised by a history of sustained sheep and cattle grazing, was assessed by monitoring ground beetle and ant communities in 18 cork oak woodlands in Sardinia, Italy, in 2016. Environmental variables and forest descriptors characterising each selected area were also quantified. Species richness (SR) and functional diversity (FD) were estimated for each taxonomical group and compared among sheep-, cattle-grazed and ungrazed sites. Multivariate analysis was conducted to investigate differences in species composition among various grazing regimes and to evaluate the influence of environmental variables on insect communities.
3. A total of 607 ground beetles (37 species) and 14,492 ants (35 species) were recorded. Sheep-grazed sites showed the highest species richness (SR) and FD for both taxa. Significant differences were found in beetle and ant assemblages among different grazing regimes. Environmental variables significantly influenced community composition. In particular, altitude and tree density were found to significantly affect both ground beetle and ant composition.
4. Our findings suggest that grazing influences arthropod communities by increasing habitat diversity and biodiversity, particularly in sheep-grazed sites, and indicate that ground beetles and ants are valuable indicators for tracking land-use changes through their population composition.

KEYWORDS

agroforestry, biodiversity, Carabidae, Formicidae

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INTRODUCTION

Grazing and agroforestry in Mediterranean landscapes

Managed grazing plays a significant role in shaping European landscapes, particularly in areas dominated by grasslands. Grazing management has been shown to have a substantial effect on habitat functionality, with pasture and/or grazing intensification and abandonment being the most significant factors (Hempel et al., 2025; Schneider & Hering, 2024; Zhang et al., 2023). Intensified production, driven by economic pressures and EU policies, has negative effects on biodiversity and leads to increased emissions (Bellarby et al., 2013; Humbert et al., 2021), whereas abandonment of pastures, mainly due to socioeconomic shifts, has led to a reduction in agricultural activity (Moreira et al., 2011) and can negatively impact biodiversity (Daskalova & Kamp, 2023). In light of the potential impact on a range of ecosystem services, including biodiversity, habitat conservation and the safeguarding of cultural benefits, it is essential to define grazing activities not only to enhance pasture productivity but also to preserve biodiversity, mitigate wildfire risks and maintain cultural and environmental health (Ryschawy et al., 2019). The intensification and expansion of agroforestry systems with multiple uses have been proposed as a sustainable land-use option to mitigate the effects of land degradation in the Mediterranean region (Le Houérou, 1993). The provision of ecosystem services by agroforestry systems has been demonstrated, including the maintenance of biodiversity at the level of habitats, species and genotypes (Landis, 2017), the sequestration of carbon (Montagnini & Nair, 2004), the reduction of soil erosion and pollution (Pavlidis & Tsihrintzis, 2017), the mitigation of fire risk (Biasi, Colantoni, et al., 2015) and the preservation of traditional agricultural landscapes and associated knowledge (Biasi et al., 2017; Biasi, Brunori, et al., 2015).

Cork oak woodlands: Ecological importance and threats

The cork oak (*Quercus suber* L.) agroforestry system is a human-managed landscape, originating from natural woodlands but now largely shaped by centuries of management for cork production and livestock grazing. Modern cork oak ecosystems represent a mosaic of fragmented natural remnants and extensive managed systems, making them both natural and heavily influenced by human activities (Aronson et al., 2009; Eichhorn et al., 2006). Historically, cork oak woodlands have been subject to significant disturbances, with recent times witnessing a heightened threat of deforestation (Aronson et al., 2009), with poor management and land overuse being considered key factors compromising the ecology and conservation of these woodlands (Aronson et al., 2009; Lopes-Fernandes et al., 2024; Maghnia et al., 2017).

Arthropods as bioindicators and study rationale

To evaluate the impact of management strategies, implementing targeted monitoring programmes in areas likely to be affected by human-

mediated disturbances is of primary interest. In this regard, the monitoring of arthropod communities has been demonstrated to be a highly valuable tool in Mediterranean ecosystems (Mannu et al., 2018, 2020; Verdinelli et al., 2017; Verdinelli et al., 2022). Among arthropods, insects play a fundamental role in biodiversity due to their distinctive responses to environmental stressors, making them invaluable biological indicators across diverse habitats (Gerlach et al., 2013). Additionally, insects are often employed in biomonitoring and conservation planning (Rodrigues & Brooks, 2007), as they are recognised as a cost-effective way to monitor biodiversity (Padial et al., 2012). Among insects, ground beetles (Coleoptera: Carabidae) and ants (Hymenoptera: Formicidae) are widely recognised as valuable indicators that at the same time significantly contribute to ecosystem stability and biodiversity, making them essential for sustainable conservation and habitat restoration efforts (Andersen, 2019; Folgarait, 1998; Koivula, 2011; Kotze et al., 2011; New, 2010). Ground beetles play a vital role in pest control, maintaining soil health and dispersing seeds, thereby affecting weed management (Lövei & Sunderland, 1996; Saska et al., 2019). Likewise, ants are key to nutrient cycling and seed dispersal (Hölldobler & Wilson, 1990). Studies investigating the impact of long-term pastoral use on invertebrates in cork oak woodlands are limited, with research primarily focusing on vegetation or vertebrate communities rather than on invertebrates at different trophic levels (Mannu et al., 2018; Verdinelli et al., 2017). Specifically, Gómez et al. (2003) explored ecological interactions in Mediterranean oak woodlands, providing a baseline for understanding grazing effects without targeting multi-trophic invertebrate assemblages. More recently, Concostrina-Zubiri et al. (2016) highlighted how grazing alters biocrust composition and associated microhabitats, indirectly affecting soil invertebrates. Furthermore, Frasconi Wendt et al. (2021) examined changes in functional diversity (FD) of ant communities along post-grazing succession in cork and holm oak woodlands, demonstrating that grazing intensity and abandonment significantly shape invertebrate functional structure. These studies collectively underscore the need for integrated research across multiple taxa and trophic levels to fully understand the impacts of pastoral activities on cork oak ecosystems. Consequently, a multitaxon approach could provide a more comprehensive evaluation of biodiversity, accurately capturing changes due to habitat modifications and providing data essential for ecological assessment (Hevia et al., 2016; van Klink et al., 2015). However, to better understand how communities respond to stress factors, a multidiversity approach that includes traditional diversity metrics and FD is essential for predicting how communities might respond to landscape changes. (Andersen & Majer, 2004; Mannu et al., 2020; Wan Hussin et al., 2012). Grazing influences insect communities through both direct and indirect mechanisms, such as habitat disturbance, resource availability (e.g., dung) and changes in vegetation structure and plant composition. These effects can alter species richness (SR), functional traits and community composition, as observed in different conditions worldwide (Filazzola et al., 2020; Littlewood, 2008; Littlewood et al., 2012; Maghnia et al., 2017; Mannu et al., 2018; Mannu et al., 2020).

Despite extensive research on grazing effects in grasslands, little is known about how different livestock species influence multitaxa arthropod communities in Mediterranean cork oak woodlands.

Previous studies have often concentrated on single taxa, short-term responses or broad presence–absence patterns, leaving a gap in understanding how grazing regimes affect both taxonomic and FD across groups. Moreover, cross-taxon congruence (i.e., the similarity of responses of different taxonomic groups to grazing-driven environmental gradients) has never been explicitly examined in Mediterranean oak agroforestry systems. Our study addresses these gaps by jointly analysing ground beetles and ants through an integrated multitaxa, multimetric approach. Since the long-term effects of large herbivores on ground beetle and ant communities have not been studied carefully (da Silva et al., 2008; Mannu et al., 2018; Vele et al., 2011; Verdinelli et al., 2017), we investigated the responses of these taxonomical groups to grazing in Mediterranean cork oak woodlands through a multitaxa approach. To study the impact of grazing on biodiversity within Mediterranean agroforestry systems, the specific objectives of this study were: (1) to analyse the patterns of ground beetle and ant communities in response to grazing from different herbivore species; (2) to assess whether ground beetle and ant traits could serve as reliable indicators of the main changes in community composition; (3) to identify the environmental variables that most significantly influenced insect assemblages; (4) to examine the potential overall cross-taxon congruence between ground beetle and ant communities in serving as bioindicators.

MATERIALS AND METHODS

Study area

The study was conducted in 2016 in Sardinia (Italy), which represents the main cork oak-growing region of Italy. Here, cork oak covers approximately 114,100 ha as forests (characterised by higher tree density and limited management) and 25,200 ha as woodlands (with lower tree density and more intensive management), together representing more than 80% of Italy's cork oak stands (Dettori & Filigheddu, 2016). In Sardinia, cork oak occurs in both pure stands and mixed formations with other oak species, particularly *Quercus ilex* and *Quercus pubescens*.

These forests and woodlands are traditionally managed for cork extraction and livestock grazing, reflecting a centuries-old agroforestry system. Grazing by domestic herbivores, including both small ruminants and cattle, remains a key land-use practice and is often combined with extensive agricultural activities such as pasture seeding. The region is further characterised by numerous small, privately owned properties, which have resulted in intense forest fragmentation. Consequently, land-use intensity and management practices exert a marked influence on stand structure and understory vegetation.

A total of 18 sampling sites were selected across ~250 km². Sites within the study area were selected at a minimum distance of 1.5 km from one another (range 1.5–18 km), ensuring a comprehensive representation of a grazing regime across a minimum area of 3 ha (Figure 1; Appendix S1).

Sites were assigned to one of three grazing categories: non-grazed (NG = 7 sites), cattle-grazed (CG = 6 sites) and sheep-grazed (SG = 5 sites). In this study, grazing treatments refer explicitly to managed live-stock grazing by domestic sheep or cattle. All ungrazed sites were free of domestic herbivores, although wild ungulates such as deer were occasionally present at low, sporadic levels. These incidental occurrences did not produce sustained grazing pressure comparable to managed pastoral activity and were therefore not considered part of the grazing treatments. Managed grazing constitutes the traditional land-use practice within these sites. Although the precise duration of grazing at each site is not officially documented, the classification of them into grazed and ungrazed categories was reliably supported by historical land-use patterns, local knowledge and the Livestock Index. Grazed sites are characterised by the everyday and ongoing use of soil as pasture, reflecting their traditional role in zootechnical production, which has persisted for decades or more. In contrast, ungrazed sites have been excluded from grazing for over 30 years and are primarily managed for cork oak production, as they are associated with higher cork quality and economic value. This long-term exclusion from grazing has been confirmed through consistent absence of domestic herbivores, direct interviews with local farmers and corroborating historical and experimental evidence. Sardinia has a millennia-long pastoral tradition (Malavasi et al., 2023), but grazing abandonment in some cork oak stands began only in the mid-20th century, mainly due to rural depopulation and changes in management. Long-term ungrazed conditions (≥ 25 years) have been documented in fenced experimental plots and restoration areas (Scotti et al., 2005), while other studies confirm vegetation and soil changes after decades of exclusion (Alias et al., 2012; Lozano et al., 2021). These sources, together with local testimonies, validate that the sites classified as ungrazed have been free from livestock for over 30 years.

Although all selected ungrazed (NG) sites were characterised by the absence of small (e.g., dairy sheep) and large herbivores (e.g., beef cattle), the presence of wild animal species such as deer and other browsers occurred sporadically. At all the grazed sites, animals had unrestricted and uninterrupted access to a variety of feed resources, including grasses, shrubs and trees. Although the specific stocking rate in Sardinia has not been precisely documented, sites were selected based on input from both local shepherds and the Livestock Index. The Livestock Index provides an estimate of the animal stocking rate, measured as the number of animals per hectare for each ruminant species at the municipality level. This index was derived from official data from the Italian Statistical Institute on animal breeding at the municipality level on the island (Canalis, 2017). At the selected sites, the Livestock Index ranged from 1 (low to intermediate level) to 3 sheep per hectare (high level) and from 0.1 (intermediate to high level) to 0.5 cattle per hectare (high level) in SG and CG sites, respectively (Canalis, 2017).

Environmental variables

The following environmental variables were either measured or estimated at each site: (1) altitude; (2) tree canopy cover; (3) absolute

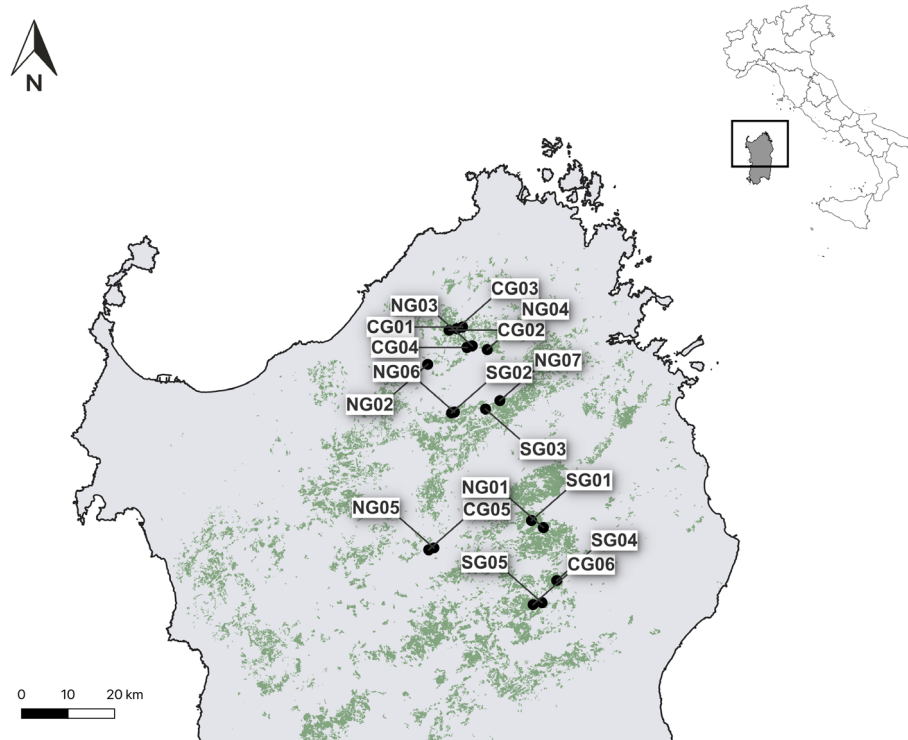


FIGURE 1 Map of North Sardinia with marked distribution of cork oak forests, and the 18 sampling units in cattle-grazed (CG), non-grazed (NG) and sheep-grazed (SG) sites.

density of trees per hectare; (4) average tree diameter at breast-high at 1.30 m above the ground (DBH); (5) average tree height; (6) shrub cover; (7) understory vegetation cover. The altitude of each sampling site was measured by using a digital altimeter with a precision of approximately 1 m. Tree canopy cover, representing the vertical projection of tree crowns on the ground, was estimated using high-resolution satellite images (4800×2718 pixels) downloaded from Google Earth Pro (available online at <http://earth.google.com>). All photos were edited separately using the GIMP 2.8 software, available online at <http://www.gimp.org>. Tree canopies were manually selected, and the area not covered by tree crowns was removed to obtain black-and-white images with black pixels representing tree crowns. Forest canopy cover was finally estimated by dividing the number of black pixels by the total number of pixels in black-and-white images (Stewart et al., 2007). The density of trees per hectare was calculated using the point-centred quarter method (Cottam & Curtis, 1956). During the spring, eight sampling points were randomly selected along a transect approximately 100 m in length at each site. Sampling points were divided into four quadrants based on the main cardinal directions. The tree closest to the point in each quadrant was identified, and the distance between the central point and the selected tree was measured (Cottam & Curtis, 1956). The absolute density λ was determined as follows:

$$\lambda = \frac{1}{\left(\frac{\sum_{i=1}^n \sum_{j=1}^4 \times R_{ij}}{4n} \right)^2},$$

where n is the number of sample points along the transect, i is a particular sampling point, j is a quarter at a transect point and R_{ij} is the point-to-tree distance at the point i in the quarter j (Mitchell, 2007). All trees identified through the point-centred quarter method approach were measured to estimate their DBH and height. Shrub cover was visually estimated using an ordinal scale (0–5), following the principle of Daubenmire's cover class method, which assigns vegetation cover to broad categories rather than exact percentages to improve consistency and efficiency in field assessments (Daubenmire, 1959). Finally, the vegetation cover (i.e., the percentage of herbs, grass and other herbaceous plants covering the soil) was calculated using object-based image analysis in eCognition® Developer software (Trimble Geospatial, Munich, Germany). During the spring, three pictures per site with a minimum resolution of 5 megapixels were taken from approximately 1.5 m above the ground to capture vegetation within a roughly 1 m^2 area. All photos were taken in the morning to reduce variation caused by different lighting conditions. Pictures were digitised as PNG files and imported into the analysis software. Image segmentation is the process of dividing an image into meaningful units (i.e., segments) by grouping pixels based on attributes such as colour, shape and texture, thereby allowing software to identify distinct objects, such as plants or bare soil (Luscier et al., 2006). After segmentation, a five-category class hierarchy (i.e., herbs, grass, other plants, litter, bare ground) was created to quantify the percentage of each vegetation category. At least 100 segments per category were manually sampled and classified into one of the five categories. The remaining segments were assigned to one

of the predefined classes using a fuzzy-logic algorithm based on their attribute similarities to the user-defined segments sampled for each class. The vegetation cover was calculated by summing the estimated values for herbaceous plants, including herbs, grasses and other similar species, and expressed as a percentage in relation to the square metre analysed.

Insect sampling and identification

Insects were sampled using pitfall traps, a widely recognised method for capturing both ground beetles (Lövei & Sunderland, 1996) and ground-dwelling ants (Sheikh et al., 2018). Each trap consisted of a plastic cup (7 cm diameter, 11.8 cm height) filled with 150 mL of a water–monopropylene glycol solution (5:1; v/v) to preserve specimens and minimise evaporation.

At each site (i.e., experimental unit), 10 pitfall traps were placed at 10 m intervals along a 100 m transect corresponding to that already used for vegetation cover estimation to ensure spatial consistency between faunal and vegetation sampling. The vegetation surrounding the traps was left undisturbed to prevent interference with trapping efficiency. Three sampling periods were considered in total, one in each season: spring (May), summer (July) and autumn (October). For each two-week sampling period, pitfall traps were activated in the field, checked and emptied weekly to prevent trap saturation. Captured specimens were transferred to 90% ethanol for later identification.

Ground beetles (Carabidae) were identified to species level following Porta (1934), with nomenclature updated according to Homburg et al. (2014). For ants (Formicidae), only the worker caste was considered in the analyses (Appendix S2), and species nomenclature followed AntWiki (2026). Other non-target invertebrate taxa were indeed collected in the pitfall traps; however, they were not included in the analysis because our expertise was limited to ground beetles and ants. The remaining taxa represented highly heterogeneous groups spanning different taxonomic ranks, making meaningful comparisons beyond the scope of this study.

SR and FD

The SR and the FD were estimated for both Carabidae and Formicidae. The SR is a standard index for measuring diversity and was calculated separately for Carabidae and Formicidae based on the total number of species present at each site. FD measures the extent of complementarity among species by considering ecological or functional traits that are associated with each species. FD was estimated separately for ground beetles and ants at each sampling site by calculating the functional dispersion (FDis) index, following the methodology proposed by Laliberté and Legendre (2010). The FDis index represents the mean distance of each species to the basal-area-weighted centroid of all species in functional trait space, and it has been employed to evaluate the functional dissimilarity (FD) of

different target groups in various environmental conditions (Laliberté & Legendre, 2010). For ground beetles, the mean body length, the hind-wing morphology and the diet were selected as functional traits because they are directly related to the species' ability to move and acquire resources (Homburg et al., 2014). For ants, the worker size, the worker polymorphism, the type of diet, the behavioural dominance, the number of nests per colony, the number of queens per colony and the type of colony foundation were considered as they better characterise the different dimensions of their functional niche (Arnan et al., 2014). Traits for ground beetles and ants (Table 1) were obtained from databases present in the available literature (Arcos & García, 2023; Arnan et al., 2012; Arnan et al., 2014; Arnan et al., 2017; Boet et al., 2020; Homburg et al., 2014; Retana et al., 2015; Scupola, 2018; Seifert, 2007).

Statistical analyses

All statistical analyses were carried out in R version 4.3.2 (R Core Team, 2023). To maintain independence among replicates and avoid pseudoreplication, pitfall trap data were pooled within each transect (i.e., site) across traps and sampling periods. As a result, all subsequent analyses were conducted at the site level ($n = 18$). FDis index was computed using the FD package, version 1.0–12.3 (Laliberté & Shipley, 2011) in R software (R Core Team, 2023).

Differences in SR and FDis among grazing treatments (NG, CG, SG) were tested using the Kruskal–Wallis test, followed by Bonferroni-corrected pairwise comparisons ($\alpha = 0.05$).

Ground beetle abundance data were $\log(x + 1)$ -transformed to reduce the influence of highly abundant species. For ants, abundance was not used due to their social nature (Wilson & Hölldobler, 2005). Instead, we calculated the total number of unique occurrences (i.e., the number of pitfall traps in which each species was detected across the sampling period). Data on ants (i.e., occurrences) and ground beetles (i.e., abundance) were both aggregated at the site level before analysis.

Prior to ordination, spatial autocorrelation in community data was tested separately for ground beetles and ants using Mantel tests (Spearman correlation, 9999 permutations) on Bray–Curtis dissimilarity and geographic distance matrices. No significant autocorrelation was detected (ground beetles: $\rho = 0.05$, $p = 0.34$; ants: $\rho = 0.17$, $p = 0.09$), and no spatial structure was included in subsequent models. Only species contributing at least 1% to overall abundance (ground beetles) or occurrence (ants) were retained in the community matrices.

Non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities was used to visualise variation in ground beetle and ant assemblages among different grazing regimes using the metaMDS function in the *vegan* package, version 2.6–6.1 (Oksanen et al., 2022). Permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations was used to test for differences among grazing treatments (adonis function in *vegan* package). To identify species contributing most to among-treatment dissimilarities, similarity percentage analysis (SIMPER) was performed (simper

TABLE 1 List and description of ground beetle and ant traits considered to estimate functional diversity.

| Taxonomical group | Trait | Data type | Measure ^a | Unit | Description |
|-------------------|---------------------------------|--------------|----------------------|--------------------------------------|---|
| Ground beetles | Mean body size (BS) | Quantitative | Continuous | mm | Distance from the tip of the mandibles to the tip of the elytra |
| | Hind-wing morphology (HM) | Qualitative | Ordinal | 1 | Winged (W) |
| | | | | 2 | Dimorphic (Dim) |
| | | | | 3 | Short-winged or wingless (SW) |
| | Diet (D) | Qualitative | Ordinal | 1 | Herbivore (Her) |
| | | | | 2 | Omnivore (Omn) |
| 3 | | | | Predator (Pr) | |
| Ants | Worker size (WS) | Quantitative | Continuous | mm | Distance from the tip of the mandibles to the tip of the gaster |
| | Worker polymorphism (WP) | Qualitative | Ordinal | 1 | Low polymorphism |
| | | | | 2 | Medium polymorphism |
| | | | | 3 | High polymorphism |
| | Diet (D) | Qualitative | Ordinal | 1 | Generalist (Gen) |
| | | | | 2 | Mainly liquid feeder (LF) |
| | | | | 3 | Predator/liquid feeder (PLF) |
| | | | | 4 | Strictly predator (P) |
| | | | | 5 | Seed harvester (SH) |
| | Behavioural dominance (BD) | Qualitative | Binary | 1 | Dominant (Dom) |
| | | | | 2 | Subordinate (Sub) |
| | Number of nests per colony (nN) | Qualitative | Ordinal | 1 | Monodomy (Md) |
| | | | | 2 | Both monodomy and polydomy (MPd) |
| | | | | 3 | Polydomy (Pd) |
| | Number of queens (nQ) | Qualitative | Ordinal | 1 | Monogyny (Mg) |
| | | | | 2 | Both monogyny and polygyny (MPg) |
| | | | | 3 | Polygyny (Pg) |
| | Colony foundation (CF) | Qualitative | Ordinal | 1 | Dependent (Fd) |
| 2 | | | | Both dependent and independent (Fdi) | |
| 3 | | | | Independent (Fi) | |

^aThese traits can be continuous, ordinal or binary, and the data are treated differently before all multivariate analyses.

function in *vegan* package). Indicator Species Analysis (ISA) (9999 permutations) was then applied to detect significant associations between individual species and grazing categories using the *indicspecies* package, version 1.7.14 (de Cáceres & Legendre, 2009).

Environmental data were fourth-root transformed before the analysis to account for heterogeneous measurement units (Borcard et al., 2011). Multicollinearity among variables was assessed using Spearman's rank correlation, and variables with $|rs| > 0.80$ were excluded. Accordingly, 'absolute tree density per hectare' was removed because of its strong correlation with 'tree canopy cover' ($rs = 0.83$).

Relationships between insect communities and environmental variables were explored using two complementary approaches:

1. Distance-based redundancy analysis (db-RDA) – Bray–Curtis dissimilarity matrices were computed separately for ground beetles (log-transformed abundance data) and ants (occurrence data). These matrices were subjected to principal coordinates analysis

(PCoA), followed by constrained ordination against environmental variables using the *capscale* function in the *vegan* package. The significance of predictors was assessed using Monte Carlo permutation tests (9999 permutations).

2. Procrustes analysis: NMDS ordinations of ground beetle and ant community data were superimposed on the NMDS ordination of environmental variables (Bray–Curtis on fourth-root-transformed data), using the *protest* function in the *vegan* package. This analysis tested for congruence between community structure and environmental gradients (Peres-Neto & Jackson, 2001).

RESULTS

A total of 607 specimens belonging to 37 species of ground beetles were collected during the sampling period (Appendix S3). The most

abundant species were *Calosoma sycophanta*, *Percus strictus*, *Trechus quadristriatus* and *Harpalus tardus*, which contributed 22.41%, 18.78%, 9.06% and 8.90% of the total number of ground beetles captured, respectively. *Calosoma sycophanta*, *Carabus morbillosus*, *H. tardus*, *Laemostenus complanatus*, *P. strictus* and *T. quadristriatus* were shared among SG, CG and NG sites. In contrast, five of the total captured species were exclusively collected at grazed sites (i.e., *Amara ovata*, *Calathus cinctus*, *H. attenuatus*, *Nebria brevicollis*, *Ophonus diffinis*).

Throughout the sampling period, a total of 14,492 ant workers were captured, representing 2640 occurrences and 35 species (Appendix S4). The most common species were *Crematogaster scutellaris*, *Aphaenogaster spinosa*, *Camponotus aethiops* and *Aphaenogaster ichnusa*, accounting for 21.25%, 15.64%, 10.98% and 7.95% of the total occurrences, respectively. Out of the 35 species sampled, 22 were found in all grazing regimes (Appendix S4). Additionally, *Lasius niger*, *Myrmecina graminicola* and *Pheidole pallidula* were only collected in the NG sites, while *Temnothorax sardous* was exclusively found in the SG sites.

Differences in SR among different grazing regimes were found for both ground beetles ($X^2 = 8.98$, $df = 2$, $p = 0.01$) and ants ($X^2 = 6.14$, $df = 2$, $p = 0.05$) (Figure 2). SG sites exhibited a significantly higher richness of ground beetle species (mean \pm SE: 11.60 ± 1.44) than CG (mean \pm SE: 6.17 ± 0.87) and NG (mean \pm SE: 5.29 ± 0.64) sites. The highest SR of ants was observed in sites characterised by a sheep grazing regime (mean \pm SE: 18.20 ± 1.16), which was significantly different from that observed in NG sites (mean \pm SE: 13.71 ± 0.92). In contrast, the SR of ants in CG sites (mean \pm SE: 15.17 ± 1.22) was not statistically different from that of SG and NG sites.

The grazing regime had a significant effect on FD as differences in the FDis index among SG, CG and NG sites were found for both ground beetles ($X^2 = 6.31$, $df = 2$, $p = 0.04$) and ants ($X^2 = 6.18$, $df = 2$, $p = 0.05$). For ground beetles, FDis in SG sites (mean \pm SE: 0.398 ± 0.010) was significantly higher than that in NG sites (mean \pm SE: 0.352 ± 0.013), whereas FDis values in CG sites (mean \pm SE: 0.374 ± 0.009) did not significantly differ from those in other grazing regimes. For ants, SG sites exhibited the highest average FDis value (mean \pm SE: 0.373 ± 0.004), which significantly differed from that estimated in CG sites (mean \pm SE: 0.331 ± 0.004). The average FDis for ants in NG sites (mean \pm SE: 0.339 ± 0.012) was instead comparable to those estimated in both SG and CG sites.

NMDS represented a good separation of ground beetle (stress = 0.17) and ant (stress = 0.16) assemblages, with a partial separation among sites typified by different grazing regimes for both insect taxonomic groups (Appendix S5).

PERMANOVA tests confirmed that the grazing regime significantly affected both ground beetle ($R^2 = 0.21$, $p = 0.02$) and ant ($R^2 = 0.22$, $p = 0.01$) assemblages. The ground beetle species composition in SG sites differed significantly from that observed in NG sites ($F = 3.00$, $R^2 = 0.23$, $p_{\text{adj}} = 0.01$). In contrast, no significant differences were found in sheep grazing versus cattle grazing ($F = 1.16$, $R^2 = 0.15$, $p_{\text{adj}} = 0.50$) and cattle grazing versus non grazing ($F = 1.37$, $R^2 = 0.11$, $p_{\text{adj}} = 0.68$) comparisons. The ant assemblage in

SG sites was found to be significantly different from those in both CG ($F = 3.06$, $R^2 = 0.55$, $p_{\text{adj}} = 0.02$) and NG ($F = 3.15$, $R^2 = 0.24$, $p_{\text{adj}} < 0.01$) sites. No significant differences in ant assemblages were found between CG and NG sites ($F = 0.33$, $R^2 = 0.03$, $p_{\text{adj}} = 1.00$).

Among ground beetles, *Phyla tethys* [Phy.tet], *Calathus ambiguus* [Cal.amb] and *Syntomus trucantellus* [Syn.tru] were selected as species typifying the sheep-grazing regime (Table 2), being at the same time among the species that significantly contributed to the dissimilarity between SG sites and other grazing regimes (Appendix S6).

No indicator species belonging to ground beetles were identified in CG and NG sites. For ants, *Messor capitatus* [Mes.cap], *Tapinoma madeirense* [Tap. mad], *Tapinoma simrothi* [Tap.sim] and *Messor minor* [Mes.min] were selected as species characterising SG sites, whereas *Camponotus lateralis* [Cam.lat] was an indicator species in NG sites (Table 2).

Comparing SG sites to NG and CG sites, *T. madeirense*, *M. capitatus*, *M. wasmanni*, *M. minor*, *Tetramorium brevicorne* and *T. simrothi* were the ant species which significantly contributed to dissimilarity between the site groups (Appendix S7). Instead, *Lasius paraliensis*, *Camponotus lateralis* and *Camponotus piceus* were the ant species responsible for the significant dissimilarity between NG and CG sites (Appendix S7).

The db-RDA analysis revealed that the responses of ground beetles and ants to environmental variables were different depending on the insect taxonomic group. In the case of ground beetles, the first and second axes of the db-RDA accounted for 31.03% of the total variation in species composition (Figure 3), and only the first canonical axis was found to be significant in the ordination bi-plot ($F = 3.92$, $p = 0.03$). The permutation test showed a significant effect of 'altitude' ($F = 3.34$, $p < 0.01$) and 'absolute density of trees' ($F = 0.34$, $p = 0.05$) in affecting ground beetle assemblages throughout the different grazing regimes (Table 3).

Observation of the db-RDA bi-plot showed a positive correlation between specific ground beetle species, including *Calathus solieri* [Cal.sol], *Harpalus tardus* [Har.tar] and *Laemostenus carinatus* [Lae.car] and altitude. This correlation was found to be accompanied by an increase in the absolute density of trees, shrubs and vegetation cover. On the contrary, the abundance of *C. sycophanta* [Cal.syc], *C. cinctus* [Cal.cin] and *Trechus quadristriatus* [Tre.qua] was found to be negatively related to the increase in altitude.

Db-RDA analysis for ant assemblages generated a similar pattern to that of ground beetles (Figure 4). A total of 40.09% of the variability was significantly explained by the first two axes (CAP1: $F = 5.64$, $p < 0.01$; CAP2: $F = 4.01$, $p = 0.01$). Ant assemblages were found to be significantly affected by 'vegetation cover' ($F = 3.55$, $p < 0.01$), 'altitude' ($F = 2.87$, $p < 0.01$) and 'absolute density of trees' ($F = 2.59$, $p = 0.01$) (Table 3). Db-RDA ordination bi-plot indicated that *Aphaenogaster spinosa* [Aph.spi], *Messor capitatus* [Mes.cap], and *Tetramorium brevicorne* [Tet.bre] were more likely to occur at a lower density of trees, shrubs and canopy cover (Figure 4). Conversely, *A. ichnusa* [Aph.ich] and *Camponotus lateralis* [Cam.lat] were promoted by a greater density of trees, shrubs and canopy cover.

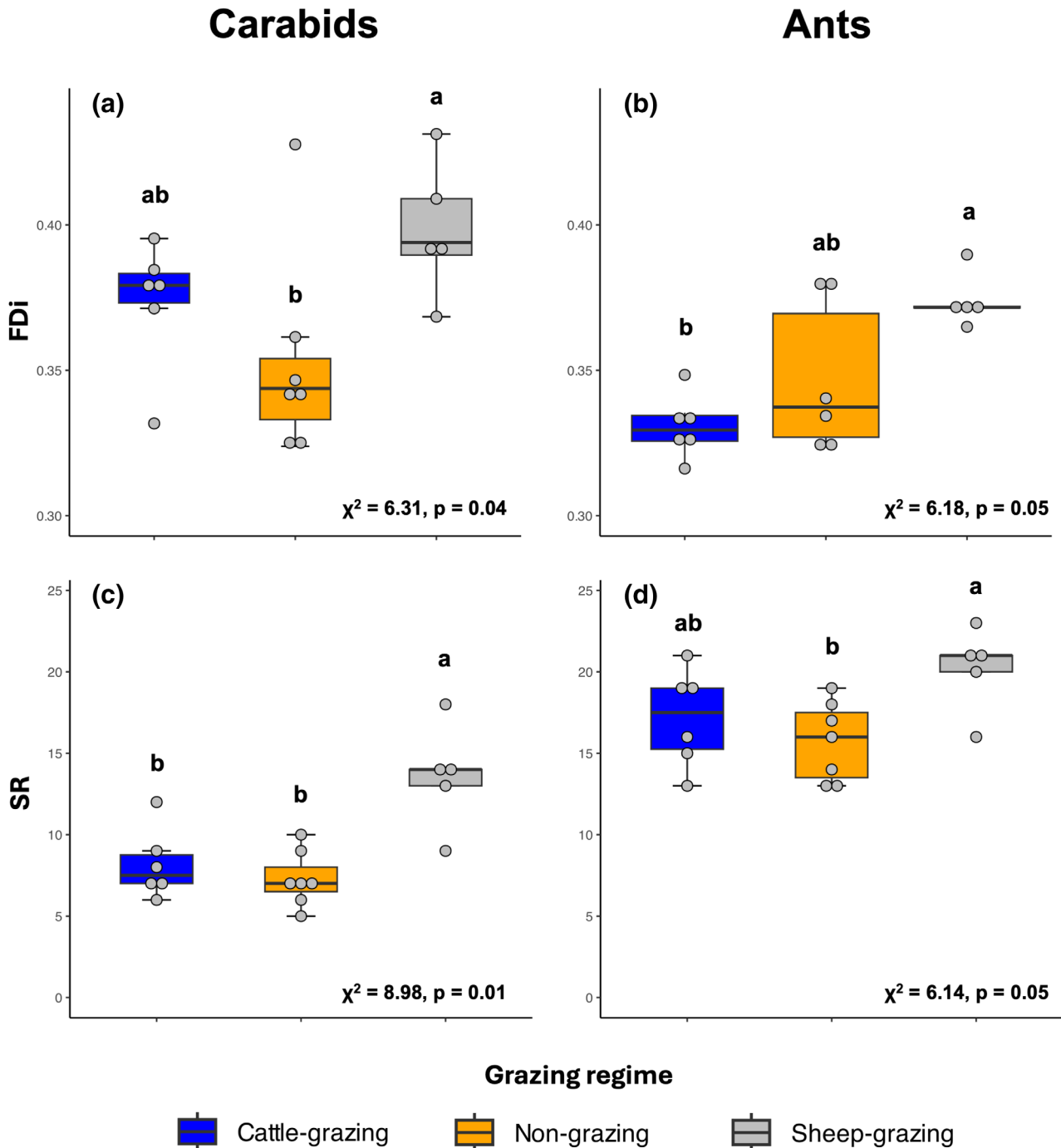


FIGURE 2 Box-plots indicating the average functional dispersion index (FDi) (a, b) and species richness (SR) (c, d) for carabids (a, c) and ants (b, d) estimated in cork oak woodlands characterised by different grazing regimes (cattle grazing = blue; non grazing = orange; sheep grazing = grey). Statistics and significance from the Kruskal-Wallis test are reported. For each index (i.e., FDi, SR) and taxonomic group (i.e., carabids, ants), different letters above the boxes indicate significant differences in metrics across grazing regimes at $\alpha \leq 0.05$.

Procrustes analysis revealed a significant correlation between the composition of ground beetle communities and environmental variables ($m^2 = 0.77, R^2 = 0.48, p = 0.03$). Additionally, a significant correlation was observed between the composition of ant communities and environmental variables ($m^2 = 0.44, R^2 = 0.75, p < 0.01$).

DISCUSSION

Unlike previous studies, which typically examined either beetles or ants in isolation, our multitaxon approach reveals that both groups respond in parallel to grazing-mediated habitat structure. This cross-taxon congruence, demonstrated here for the first time in

TABLE 2 Indicator species analysis identifying ground beetle and ant species that characterise sheep-grazing, cattle-grazing and non-grazing regimes.

| Taxonomical group | Species | Sheep grazing | | Cattle grazing | | Non grazing | |
|-------------------|---------|----------------------|------------|----------------------|------------|----------------------|------------|
| | | IndVal _{ij} | <i>p</i> * | IndVal _{ij} | <i>p</i> * | IndVal _{ij} | <i>p</i> * |
| Ground beetles | Phy.tet | 0.894 | 0.0017 | – | – | – | – |
| | Cal.amb | 0.775 | 0.0110 | – | – | – | – |
| | Syn.tru | 0.775 | 0.0123 | – | – | – | – |
| Ants | Mes.cap | 0.951 | 0.0003 | – | – | – | – |
| | Tap.sim | 0.926 | 0.0010 | – | – | – | – |
| | Tap.mad | 0.769 | 0.0160 | – | – | – | – |
| | Mes.min | 0.730 | 0.0321 | – | – | – | – |
| | Cam.lat | – | – | – | – | 0.759 | 0.0129 |

Note: IndVal_{ij} is the value indicating the species in parts per unit.

*Permutation *p*-value based on 9999 permutations.

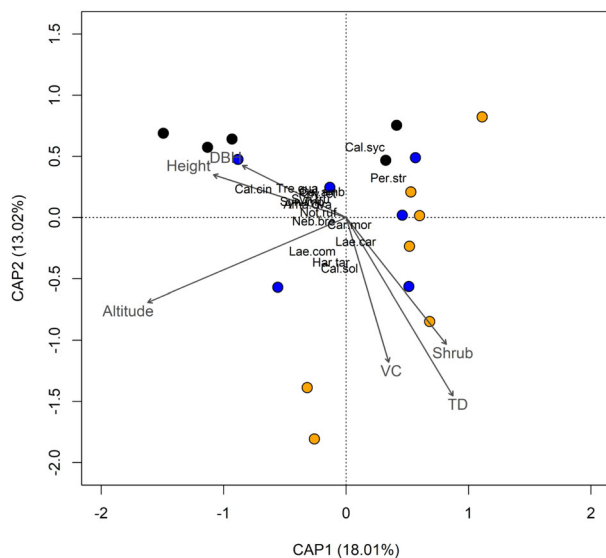


FIGURE 3 Distance-based redundancy analysis (db-RDA) ordination biplot based on ground beetle species composition as a function of environmental variables, showing the relative position of the sampling sites (coloured circles) and ground beetle species (text labels). Each circle represents the community of ground beetles caught at each site during the entire sampling period; colours indicate the different grazing regimes (black = sheep grazing; blue = cattle grazing; orange = non-grazing).

Mediterranean cork oak woodlands, provides strong support for the use of ants as a cost-effective surrogate for monitoring broader arthropod responses to land-use practices. Our findings show that grazing in Mediterranean cork oak woodlands significantly influences invertebrate communities, such as ground beetles and ants, by altering microhabitat structure and resource availability. Rather than merely mirroring previously described patterns, our results provide new evidence that different grazing regimes generate distinct habitat configurations that promote species turnover and functional diversification. Grazing can influence invertebrate assemblages through both direct disturbance and indirect modifications of vegetation structure, plant

species composition and habitat heterogeneity (Dennis et al., 2001; Morris, 2000; Woodcock et al., 2005). Differences in feeding behaviour between sheep and cattle—sheep clipping vegetation close to the ground and cattle creating more heterogeneous sward patches (Canalis, 2017; Ferreira et al., 2013; Grant et al., 1985; Rook et al., 2004)—likely produce microhabitat mosaics that affect arthropod communities differently. This variation enhances the availability of ecological niches and promotes species coexistence, in line with the habitat heterogeneity hypothesis (Pianka, 1966). By clarifying the mechanisms through which grazing shapes multi-trophic arthropod communities, our study adds mechanistic depth to earlier work and establishes a more robust ecological basis for interpreting grazing effects in Mediterranean woodlands. Consequently, grazing practices that promote a more diverse sward, such as low-intensity grazing with cattle or sheep, as opposed to no grazing, are likely to enhance invertebrate SR by increasing the availability of niches. Moderate grazing by sheep or cattle can enhance plant biodiversity by reducing the dominance of competitive species, creating microsites for seedling establishment, and maintaining an open grassland structure (Fuhlendorf & Engle, 2001; Grime, 1973; Milchunas et al., 1988; Osem et al., 2002; Peco et al., 2012).

Ground beetle assemblages are known to be affected by microhabitat variation and biotic interactions at smaller scales (e.g., ‘patchiness’) (Antvogel & Bonn, 2001; Brose, 2003; Niemelä et al., 1992), as well as by ground vegetation and litter (Koivula, 2011; Niemelä et al., 1993; Niemelä & Spence, 1994; Rainio & Niemelä, 2003). Our findings, which show that SG sites exhibit the highest ground beetle SR and an overall increase in biodiversity compared to no-grazed and CG, have significant ecological implications. Similar to previous findings that highlighted the responses of ground beetle diversity and assemblage composition to habitat heterogeneity and structural changes (Aviron et al., 2005; Magura et al., 2003; Penev, 1996; Scott & Anderson, 2003), our results show that grazing by sheep and cattle likewise influences ground beetle diversity and community structure. Although we did not test the impact of sheep and cattle co-occurring grazing on arthropod diversity, our findings

Peco, 2012). However, the duration of grazing exclusion is a key factor, and long-term or prolonged grazing exclusion (i.e., land abandonment) has been observed to result in a decrease in ant biodiversity and a shift in ant community composition (Verdinelli et al., 2022). Additionally, the natural landscape of Sardinia has been historically influenced by the activities of both domestic and wild browsers and grazers. Although the response of the ant community to grazing may seem controversial, other evidence supports the hypothesis that long-term grazing activities increase ant richness and alter the abundance of functional groups, with the ant response to grazing being independent of shrub cover (Radnan & Eldridge, 2018).

Our findings also indicated that forest descriptors exert a more pronounced effect on the ant community than the ground beetle community. The limited presence of trees and shrubs, typical of some SG areas, was found to favour thermophilic species such as *Messor* spp. (Verdinelli et al., 2022). In this regard, it is well established that forest structure and tree species have a significant impact on understory vegetation by modifying resource availability (Barbier et al., 2008). Cork oak woodlands are recognised as biodiversity hotspots (Aronson et al., 2009; Bugalho et al., 2011), supporting a rich invertebrate community (Mannu et al., 2018; Verdinelli et al., 2017). Ants are integral to food webs and ecosystem processes, and their stationary and perennial nests allow for straightforward year-round sampling. This characteristic enables a comprehensive and dynamic understanding of these ecosystems. For this reason, future research should be focused on investigating the primary drivers of ant community composition to significantly enhance our knowledge of how these communities respond to land-use changes.

The positive association we observed between grazing and the diversity of ground beetles and ants has relevant ecological and practical implications. Patterns of community change in response to structural habitat gradients—such as those produced by different grazing regimes—are well documented for both taxa (Antvogel & Bonn, 2001; Arnan et al., 2014; Niemelä et al., 1992). Because similar environmental gradients can generate comparable responses across distinct biological groups, such patterns often give rise to spatial congruence among taxa (Hevia et al., 2016). Understanding the mechanisms driving this cross-taxon congruence is essential for interpreting large-scale biodiversity patterns and for developing effective conservation strategies in the context of global change (Toranza & Arim, 2010). A typical response of ground beetles and ants to grazing suggests that pastoral land use is a significant factor contributing to changes in species composition, particularly when shifting from a non-grazing to a grazing regime. This shift is corroborated by cross-taxon analyses, which demonstrate that ant communities mirror those of ground beetles. This mirroring suggests that reducing the need for extensive taxonomic expertise could enhance the cost-effectiveness of ecological surveys. These findings highlight the reliability of ants as bioindicators of land-use changes and ecosystem health, which is essential for biodiversity monitoring and conservation.

CONCLUSION

This study provides the first multitaxa and functional evaluation of grazing effects on ground beetle and ant assemblages in

Mediterranean cork oak woodlands. By integrating responses across two ecologically distinct taxa, we showed that grazing can promote higher SR, FD and community turnover. These patterns indicate that grazing enhances fine-scale habitat heterogeneity, with changes in vegetation structure and microhabitat availability emerging as the primary drivers of arthropod responses.

The strong congruence observed between different taxa suggests that similar structural habitat gradients influence both beetle and ant communities. This cross-taxon consistency highlights the potential of some arthropod groups, such as ants, to serve as effective, cost-efficient surrogates for broader arthropod monitoring in Mediterranean agroforestry systems. The identification of indicator species linked to specific grazing regimes further enhances their value as bioindicators of land-use change.

Overall, our results demonstrate that traditional, low-intensity grazing practices help maintain diverse multi-trophic insect communities by sustaining habitat heterogeneity at multiple spatial scales. These findings emphasise the importance of preserving heterogeneous grazing mosaics within cork oak landscapes and highlight the need for further research into the mechanisms governing arthropod community responses to changing management regimes. Such insights are essential for guiding conservation strategies to safeguard insect diversity in human-influenced Mediterranean ecosystems.

AUTHOR CONTRIBUTIONS

Marcello Verdinelli: Conceptualization; data curation; funding acquisition; investigation; supervision; visualization; writing – original draft; writing – review and editing. **Maria Leonarda Fadda:** Data curation; investigation. **Stefano Arrizza:** Data curation; investigation. **Roberto Mannu:** Conceptualization; formal analysis; investigation; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

All datasets generated and analysed during this study are publicly available through Dryad at <https://doi.org/10.5061/dryad.j9kd51csz> (Verdinelli et al., 2026), in accordance with the journal's data-sharing policy.

ETHICS STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the Journal's author guidelines page, have been adhered to.

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SUPPORTING INFORMATION

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

Appendix S1. Coordinates and forest descriptors for the 18 sampling units in cattle-grazed (CG), non-grazed (NG) and sheep-grazed (SG) sites.

Appendix S2. Ant dichotomous key reference list.

Appendix S3. Ground beetle species collected during the survey in non-grazed sites (NG) and in sites grazed by cattle (CG) and sheep (SG). Abundance and functional traits are reported per each species: Mean body size (BS) (mm), Hind-wing morphology (HM: 1 = winged;

2 = dimorphic; 3 = short-winged or wingless), Diet (D: 1 = herbivore; 2 = omnivore; 3 = predator).

Appendix S4. Ant species collected during the survey in non-grazed sites (NG) and in sites grazed by cattle (CG) and sheep (SG). Abundances (N) and occurrences (Oc) are reported. Ant traits: Worker size (WS), Worker polymorphism (WP), Diet (D), Behavioural dominance (BD), Number of nests per colony (nN), Number of queens (nQ), Colony foundation (CF). For ant traits in species for which no data are reported in the literature, 10 workers per species were randomly selected and measured to determine the WS; the mean of these measurements was used as a value for each species.

Appendix S5. Non-metric multidimensional scaling (NMDS) ordination plots of sites based on (A) ground beetle abundances and (B) ant occurrences. Ground beetle abundance data were transformed using the $\log(x + 1)$ function before analysis. Each circle represents the community of ground beetles and ants caught at each site during the entire sampling period, and colours indicate the different grazing regimes (black = sheep grazing; blue = cattle grazing; orange = non grazing).

Appendix S6. Similarity percentage (SIMPER) analysis identifying ground beetle species most contributing to Bray–Curtis dissimilarities: (a) sheep grazing versus non grazing, (b) sheep grazing versus cattle grazing; (c) non grazing versus cattle grazing.

Appendix S7. Similarity percentage (SIMPER) analysis identifying ant species most contributing to Bray–Curtis dissimilarities: (a) sheep grazing versus non grazing, (b) sheep grazing versus cattle grazing; (c) non grazing versus cattle grazing.

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