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Protected habitats support bats in Mediterranean dry grasslands

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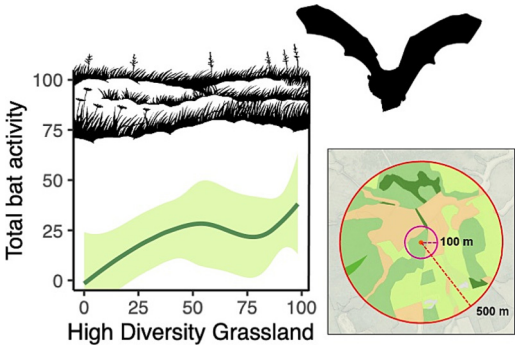
HIGHLIGHTS

- We investigated ecological drivers of bat activity in a Mediterranean grassland ecosystem.
- We focused on the effects of landscape composition and of protected habitats on bats.
- Landscape composition and terrain factors shaped activity of bats from all guilds.
- Bat assemblages significantly shifted from natural to anthropogenic grasslands.
- EU-listed high-diversity grasslands sustain bats by boosting activity levels.

GRAPHICAL ABSTRACT



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ABSTRACT

The replacement of natural habitats by urbanization and agricultural land reclamation is one of the main drivers of biodiversity loss. Among European habitat types, natural grasslands are particularly prone to anthropogenic pressures, being also recognized as conservation priorities within the Habitats Directive. Nonetheless, little is known on the relationship between grasslands, their conservation quality, and most animals' taxa that may rely upon them. Here we focus on the role of Mediterranean dry grasslands protected by the EU legislation in sustaining bat populations, setting our study in the biodiversity hotspot of Mediterranean Italy. By conducting acoustic surveillance at 48 sites within a protected area devoted to conserve natural and semi-natural grasslands, we found that all the bat species found in the area are regular exploiters of such open environments. Grassland conservation quality, in terms of extent of high-diversity protected habitats, was the key factor shaping the use of grasslands by bats of all the considered guilds, together with several terrain and landscape features, which showed more guild-specific effects. Moreover, our results indicate that bat assemblages are functionally shifted along an ecological gradient from highly modified to well-conserved grassland sites, indicating a prevalence of opportunistic taxa in the former, and higher abundance of species of conservation concern in the latter. Overall, we demonstrate that the effects of EU-listed habitats may extend also onto bats in the case of Mediterranean dry grasslands, highlighting the importance of preserving such habitats as a tool for conserving highly mobile species.

1. Introduction

The replacement of natural habitats with anthropogenic ones through urbanization and agricultural extensification is one of the main drivers of

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biodiversity loss worldwide. Such processes have been historically most relevant in geographical areas with high and ancient presence of human settlements such as the Mediterranean basin, which conversely is also a biodiversity hotspot within the Palearctic region (Medail and Quezel, 1999). The gap between natural and anthropogenic areas in providing suitable space to wildlife has also recently been widened by agricultural intensification, a set of practices that relies on biologically simplified crop monocultures and harvest automatization, both factors proved as detrimental to the persistence of wildlife (Kehoe et al., 2017).

Despite a rich body of literature on the loss of natural habitats due to agriculture land reclamation at the expense of e.g., forest and wetland ecosystems (Ballut-Dajud et al., 2022; Curtis et al., 2018), a predominant portion of what nowadays is intensive cropland has actually replaced natural (steppes) and semi-natural (pastures and meadows) open environments, i.e. dry grasslands, throughout a process occurring in Europe since the Holocene (Gang et al., 2014; Lark et al., 2020; White et al., 2000). European natural and semi-natural dry grasslands have been furtherly reduced in extent throughout the 20th century, due to land abandonment and subsequent encroachment by shrublands and forests (Emanuelsson, 2008). Nonetheless, European dry grasslands are home to an extremely rich and unique set of herbaceous plant species, as well as specialized insect, bird and mammal communities (Goriup and Batten, 1990; Pärtel et al., 2005) that rely on such fragile environments. Due to the impressive biodiversity they host and their implicit vulnerability to anthropogenic pressures, European dry grasslands are recognized as conservation priority habitats of community interest within the EU Habitats Directive, which thus grants for their legal protection and identifies these habitats as key to the implementation of the Natura2000 network (Evans, 2012).

Among the animal communities hosted by European dry grasslands, great attention has been focused on insects (especially butterflies), leaving huge knowledge gaps on most taxa that occur in these habitats and may play a key role by occupying other trophic levels (Polus et al., 2007; Warren et al., 2021). Among these, bats certainly represent an understudied group in terms of their relationship with open environments, that are usually deemed as poorly attractive to these mammals (Treitler et al., 2016). Bats are key elements in natural and anthropogenic ecosystems: their high mobility and multi-habitat specialization make bats providers of vital ecosystem services and ecological connections among several habitat types, even though they are considered as mostly associated with forest and wetland areas (Ghanem and Voigt, 2012). Nonetheless, an increasing body of literature highlights how bats are regular exploiters of anthropogenic open environments, such as cropland and pastures and urban green spaces, providing essential ecosystem services to agriculture too (Finch et al., 2020; Fuentes-Montemayor et al., 2013; Kalda et al., 2015). As such, it is plausible that the relationship between bats and grasslands is actually hardwired in bats' ecological preferences, dating back to a time before the advent of agriculture and the replacement of grasslands by cropland, as also suggested for the association between bats and domestic cattle in replacement of herds of large wild herbivores (Ancillotto et al., 2017; Hearn, 2015).

As for other anthropogenic habitat types, e.g. urban areas, species adaptability to habitat modifications may vary according to biological and functional traits, reflecting the ecological relationships between a species and its environment, and resulting in a "filtering effect" and modified assemblages (Aronson et al., 2016; Santini et al., 2019). As for bats, two main functional guilds may be recognized, based on bioacoustic and morphological traits (Denzinger and Schnitzler, 2013), corresponding to species adapted to fly in open environments (Open/edge foragers) and others more strictly associated with structurally complex environments such as forests and shrubland (Narrow space foragers). The two guilds also differ in their susceptibility to several anthropogenic pressures, e.g. wildfire and urbanization, in turn affecting their extinction risk (Ancillotto et al., 2021; Bosso et al., 2018). These guilds are frequently adopted in bat studies, as they feature distinct ecological relationships with environmental structure and complexity, with narrow space foragers exploiting more complex (cluttered) environments by gleaning prey from vegetation, while open/edge foragers tend to fly far from obstacles at higher elevation from the ground, hawking upon prey in flight.

Here we investigate the role of well-conserved Mediterranean dry grasslands in sustaining bat populations, particularly focusing on the potential role of protected habitats listed within the EU Habitats Directive, in providing profitable resources to bats in open environments. At the same time we assess the influence of landscape composition in shaping the importance of grasslands to bats, critical for informing both management and species monitoring. Specifically, we first compare bat activity and assemblage structure across different habitat-types, including grasslands, and then focus on the latter to identify factors that drive local habitat use within grasslands. We hypothesize that bats in areas dominated by grasslands are adapted to exploit such habitats, provided that these are well conserved, and thus predict that open-space foragers will be disproportionately active at grassland sites than narrow-space foragers, which in contrast are expected to be more active at wooded sites. We also expect that the amounts of intensive cropland and protected grassland habitats will diverge in influencing activity levels and composition of local bat assemblages, with lower activity and diversity in more intensively managed/modified open habitats than in well-conserved natural dry grasslands. Moreover, we expect that such relationship may also vary as a function of species' traits and their functional role within the community, expecting contrasting preferences between different bat guilds and functional shifts at the assemblage level as a function of landscape composition.

2. Materials and methods

2.1. Study area

We conducted our study in the Alta Murgia National Park and its immediate surroundings (Fig. 1), in southern Italy. The Italian Peninsula is a well-known biodiversity hotspot, also for bats (Mayer et al., 2007), and its southern regions are particularly rich in endemic taxa and poorly known ecosystems, including the dry grassland landscape of the "Murgia Alta" Natura2000 protected area i.e., one of the best conserved and continuous natural grassland areas in the Western Mediterranean basin. The Park was established in 2004, especially for conserving the natural and traditional landscapes of Mediterranean dry grassland ecosystems, an action urgently needed in response to the fast replacement of such environments with intensive cropland that locally occurred in the 90s'. Ranging from 300 to 700 m a.s.l., Alta Murgia is characterized by its deep and compact platform of Cretaceous limestone, with very shallow and rocky soils and total lack of surface watercourses. The climate is typically sub-Mediterranean, with mean annual variation from 7 °C in January to 25 °C in July/August and rainfall concentrated in autumn-winter season, with average values of 570 to 700 mm/year and snow occasionally occurring above 500 m a.s.l. With the exception of residual patches of downy oak (*Quercus pubescens*) forests and conifer plantations, the upper part of Alta Murgia is extensively covered by annual crops and semi-natural dry grasslands. Grassland habitats are partially listed in Annex I of the Habitats Directive (HD), namely as semi-natural dry grasslands on calcareous substrates (HD code: 6210), pseudo-steppe with grasses and annuals of the Thero-Brachypodietea (6220), and Eastern sub-Mediterranean dry grasslands (62A0). These grassland types are characterized by their high value of plant species richness, also hosting a remarkable set of endemic and rare species (Forte et al., 2005). As for bats, fourteen species of bats are known to occur in the area, yet five are relatively rare and/or restricted to single sites or to locally poorly represented habitat types such as woodland and water sites (*Rhinolophus hipposideros*, *R. euryale*, *Myotis emarginatus*, *M. daubentonii* and *M. myotis*).

2.2. Bat sampling and identification

We followed a semi-stratified sampling design to deploy automatic ultrasound recorders (Audiomoth 2.0, by OpenAcoustics) according to the availability of natural and semi-natural habitat-types, classified as either

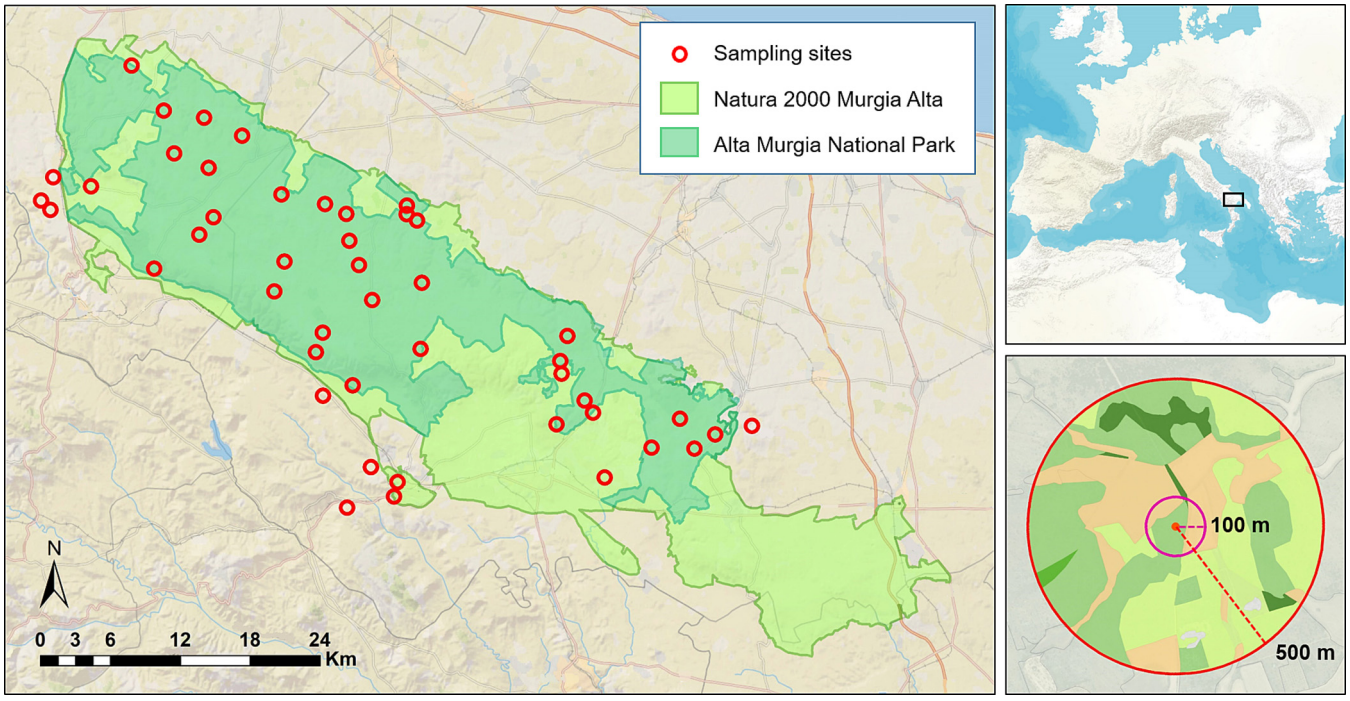

Fig. 1. Map of study area (on the left), showing location of sampling sites (n = 48) within the protected area of Alta Murgia National Park and Natura 2000 Murgia Alta conservation area. Right panels show study area location in southern Italy (upper panel) and an example of the two spatial scales (100 and 500 m; lower panel) at which landscape composition was investigated in the study.

forest (1.6 %, including broadleaved standings of *Q. pubescens*, with minor occurrence of conifer plantations and shrublands), grassland (14.9 %, including synanthropic herbaceous vegetation and protected dry grasslands), and wetlands (<0.1 % of cover, all consisting in semi-natural or artificial ponds); we also located additional sampling sites within more anthropogenic habitat types, classified as cropland (83.4 %, mainly consisting in intensive cereal crops). In total, we located 48 sampling sites across the study area, with a minimum distance of 1.1 km from each other (Fig. 1). Recording devices were secured to vegetation at ca. 1.5 m from the ground, with an upward 45° inclination, pointing away from cluttered vegetation; recording was scheduled as continuous from sunset to dawn (8 h), at a sampling rate of 380 kHz, with a file duration of 10 s followed by 50 s of pause, i.e. allowing to standardize bat activity levels as 'minutes with activity' occurrences; recordings were saved as .wav files on SD memory cards. Each site was sampled once, in randomized order, between May and September 2022, i.e. covering the seasonal peak of activity for bats in the area. Each sample consisted in one recording session per site, lasting one night. Sampling nights were evenly distributed throughout the study period, with 5 devices being simultaneously deployed in the field approximately every 15 days. Recording sessions were all conducted under good weather conditions, i.e. with no precipitation and with minimum night temperature well >10 °C, in order to ensure comparably favorable conditions to bats.

Analysis of recordings was manually conducted in BatSound 4.12 (Pettersson Elektronik AB), following the combined approach used by Ewert et al. (2023) for identification. Calls were assigned to species or species groups, e.g. for calls belonging to most *Myotis* spp.; we furtherly refined identifications by screening the known bat checklist provided by the National Park, as well as recent nationwide distributional reviews (Loy et al., 2019). Calls were also grouped into the two distinct eco-morphological guilds i.e., open space/edge foragers characterized by loud calls emitted at low-to-medium frequencies and by a long-and-narrow wing morphology (genera: *Pipistrellus*, *Hypsugo*, *Eptesicus*, *Miniopterus*, and *Tadarida*), and narrow space foragers echolocating with low-intensity calls, usually at higher frequencies, and featuring proportionally shorter and wider wings (genera: *Rhinolophus*, *Plecotus*, and *Myotis*).

2.3. Land cover mapping

We quantified land cover composition (as percent of different land cover types) at two spatial scales around recorders, corresponding to two concentric radii of 100 and 500 m respectively, centered around each recording site. Such distances are usually adopted in bat studies, and represent two of the spatial scales at which bats usually respond to landscape composition and configuration, probably as a consequence of travelled distances and size of core foraging areas for most species (Azam et al., 2016; Falcão et al., 2021; Lookingbill et al., 2010). Land cover types were mapped and classified by means of photointerpretation upon the most recent available orthophotographs (year 2019; https://pugliacon.regione.puglia.it/), and validated in the field, resulting in a shapefile vector layer processed in QGis 3.22. According to the need to integrate land use taxonomy with information on vegetation vertical structure, considered to represent an important feature for bats, we selected and quantified 10 main land cover classes, and namely i) water bodies, ii) conifer plantations, iii) broadleaved woodland, iv) Mediterranean shrubland, v) grassland with interspersed trees, vi) natural and semi-natural grassland, vii) wood-crop, viii) vineyards, ix) annual crop, and x) ruderal (synanthropic) vegetation. We then used the proportion of land cover types to calculate land cover Shannon's diversity (H′), and to categorize each recording site as either woodland, grassland or cropland area – the latter two land covers being both considered as open environments – according to the prevalent cover (>50 % at 100 m scale). For assigning sites at one of the three selected classes, we considered as woodland classes ii and iii, cropland class ix, and grasslands classes v, vi and x. Our simplification to only three categories was justified by the extremely low amounts of some classes (namely: i, vii, viii and x) cumulatively covered, on average, 2.33 % of terrain surrounding our sampling sites within the 500 m scale (range 0–9.6 %). Within each grassland patch, we also quantified the percentage of habitats listed in Annex I of the Habitats Directive, i.e. semi-natural dry grasslands on calcareous substrates (6210), pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea* (6220), and Eastern sub-Mediterranean dry grasslands (62A0), which were all pooled together and classified as high diversity grasslands (HDG hereafter). Moreover, for each recording site, we

measured landscape features that are known to potentially influence bat activity, such as distances to caves as potential roosts and percentage of sloping terrain (>20°), which may act as corridors throughout the landscape. Sloping terrain in open environments such as our study area may provide valuable corridors to bats, since they mainly consist of ravines and karst gorges, i.e. narrow canyons that represent conspicuous linear elements in a mostly homogeneous landscape. We preliminary checked all variables for collinearity by using Spearman rank correlation tests, resulting in coefficient values between −0.5 and 0.6, thus suggesting the occurrence of no statistically acceptable correlation.

2.4. Statistical analyses

We conducted all analyses in R 4.0.3 (Team, 2013). For all tests, we considered significant results with $p < 0.05$.

2.4.1. Bat responses to landscape composition

We selected, as response variables, several indicators of bat occurrence i) total bat activity, ii) α diversity (species richness), and iii) guild-specific activity. First, to assess the role of open environments in shaping the overall patterns of bat occurrence in the study area, we tested for differences in total bat activity and α diversity (species richness) among three main habitat types categorized as wooded areas, grassland and cropland, by using generalized linear models (GLMs), adopting a binomial negative (for activity, to account for data overdispersion) and Poisson (for richness) error distributions, and a log link function, using the *MASS* package (Ripley et al., 2013), using habitat type and sampling date as fixed factors. We then ran a Tukey's post hoc test with Bonferroni correction to assess significance of differences between each pair of habitat types.

Secondly, we specifically focused on open habitats only (i.e. sites classified as either cropland or grassland in the previous analysis) to highlight drivers of bat activity in these habitat types that dominate the landscape in our study area. In this case, we adopted a set of similarly structured generalized linear or additive models (GLMs/GAMs, using the *gam* package: Hastie and Hastie, 2015) according to the expected response to variables (linear vs non-linear), using the percent amounts of different land covers around each sampling site as explanatory variables, landscape features and sampling date as covariates; since some land cover types were present at few sites (<10 %) or showed low percent cover at sites (on average, <5 % of cover at either spatial scale), we only selected, for these analyses, the amounts of cropland, wooded area, and grasslands. For these models, we used both overall bat occurrence descriptors (α diversity and total activity) as well as guild-specific activity levels. For comparability, we only ran full models, one per response variable at each spatial scale (100 vs 500 m landscapes), and considered as significant those variables whose 95 % confidence intervals on effect size did not encompass 0.

2.4.2. Composition of bat assemblages

We tested for differences in species and guild composition of bat assemblages recorded at each site by adopting a multivariate approach, using the *vegan* package (Oksanen et al., 2013). Specifically, we first normalized single-species activity levels per site by log transforming raw data, for better taking into account the occurrence of rare species in comparison to very common ones. Activity levels inferred from acoustic data are frequently used as a surrogate for abundance in bat studies, despite the risk to overestimate abundance due to potentially detect single individuals multiple times (Hazard et al., 2023; Williams-Guillén and Perfecto, 2011). Nonetheless, the high mobility of bats and the frequent use of different foraging areas by single individuals should minimize such risk, allowing using such an approach as a tool to detect anthropogenic changes to bat assemblages. We then assessed the effects of the considered covariates in shaping assemblage composition by using Canonical Correspondence Analysis to quantify the role of each environmental variable in influencing species composition within the assemblage, whose statistical significance was assessed by performing a permutation test (9999 permutations).

3. Results

Across 48 sampling sites, during a total of 23,040 min of acoustic surveillance, we recorded 2056 min of bat activity (8.9 % of recording time), belonging to 10 species/species groups (taxa, hereafter), grouped into two eco-morphological guilds (open/edge foragers: N = 1726; narrow space foragers: N = 330). Mean bat activity time per site was 42.8 min (range: 0–154), with an average of 3.3 taxa (range: 0–8) recorded at the same site. The most active bats recorded in the study area are two open/edge species, *Pipistrellus kuhlii* and *Hypsugo savii*, totaling 76.8 % of the overall occurrences, followed by *M. myotis/blythii* (11.2 %); each of the other recorded taxa (Table 1) represented <5 % of total activity.

At a coarse scale, habitat type did not affect bat α diversity ($p > 0.05$), whereas a significant effect was evident for overall bat activity levels, with significantly lower values between cropland sites in comparison to both dry grassland (Tukey's $p < 0.01$) and woodland (Tukey's $p < 0.05$) sites; no statistically significant difference was evident between woodland and dry grassland sites (Fig. 2).

Of the 48 sites, 35 were classified as open environments and thus used for testing the effects of landscape features on bats in more detail. At the 100 m spatial scale, no landscape composition variable significantly influenced bat activity levels at any level (overall and guild activity levels, and α diversity). At the 500 m spatial scale, total bat activity was positively driven by two land cover descriptors, i.e. the extent of HDG and land cover diversity, which was also the only significant predictor positively influencing local bat α diversity; two landscape elements also influenced total bat activity, with higher values at sites with more high-slope terrain and at closer distances to caves, the latter also being significant for the narrow space foragers guild. The extent of HDG (on average: 29.9 %; range: 0–81 %) also positively influenced both narrow space and open/edge foragers, with both guilds increasing their activity levels at higher proportions of HDG; specifically, activity of all taxa mostly increased at HDG percent values >25 %, with particularly low activity of narrow space foragers below such threshold (Fig. S1 in Supplementary materials). We also detected a strongly significant interaction between the amount of grassland and the proportion of HDG for narrow space foragers only, indicating an increasingly positive effect of HDG at decreasing amounts of grassland in the landscape. The extent of wooded areas (on average: 4.0 %; range: 0–38 %) positively affected open/edge foragers, and negatively affected narrow space foragers, similarly to the amounts of cropland (average: 44.2 %; range: 1.2–92.8 %) (Table 2; Fig. 3).

The CCA revealed significant associations between environmental factors and bat assemblage structure (Pillai's trace: 0.75, $p < 0.01$; Fig. 4), with the first two axes explaining 81.3 % of assemblage variation along the considered ecological features.

Assemblages were mainly separated along an axis that corresponded to a gradient from sites with a prevalence of cropland to a prevalence of semi-natural and high diversity grasslands, with an additional effect of land

Table 1
Total activity levels (as minutes) and spatial spread (as % of sites) of bat species/species groups, distinct as two eco-morphological guilds, based on acoustic monitoring of 48 sampling sites. *: species of community interest, listed within the Annex II of the EU Habitats Directive.

Species/species group	Total activity	Percent of sites (%)
Open-edge foragers guild		
Pipistrellus kuhlii	909	89.6
Hypsugo savii	643	83.3
Pipistrellus pipistrellus	47	81.3
*Miniopterus schreibersii**	79	16.7
Eptesicus serotinus	40	18.4
Tadarida teniotis	8	10.4
Narrow space foragers guild		
*Myotis myotis/blythii**	226	33.3
*Rhinolophus ferrumequinum**	49	31.3
Plecotus cf. *austriacus*	20	25.0
Unidentified *Myotis*	35	37.5

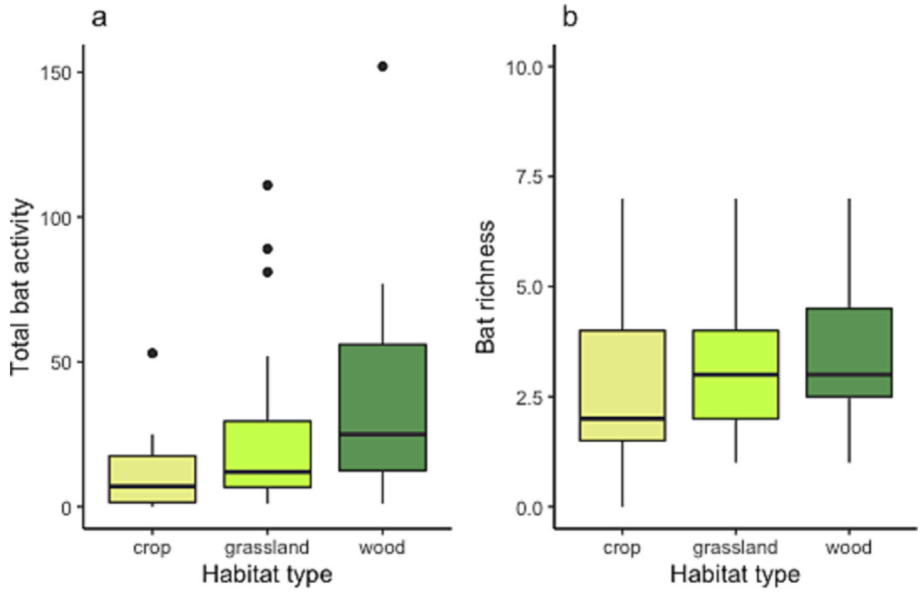

Fig. 2. Comparison of total bat activity levels (a; in minutes) and α diversity (b; as numbers of species per site) among three habitat types from the Alta Murgia National Park (Southern Italy), as assessed by autonomous acoustic sampling (n sites = 48).

cover diversity and amounts of woodland. Namely, assemblages were characterized by either species associated to more diverse and wooded areas (*Miniopterus schreibersii, Eptesicus serotinus, Pipistrellus pipistrellus*), others to more open areas with increasing proportions of HDGs (*Myotis myotis/blythii, Hypsugo savii, Tadarida teniotis*), and others to sites closer to caves (*Rhinolophus ferrumequinum*, *Plecotus* sp.) or with higher amounts of cropland (*Pipistrellus kuhlii*).

4. Discussion

Dry grassland ecosystems are recognized as fundamental areas to European biodiversity, and great attention has been recently focused on their conservation, due to their extreme past contraction and current vulnerability to anthropogenic modifications (Valkó et al., 2016). Dry grasslands host incredibly high numbers of plants and invertebrates, yet they have been poorly investigated in terms of their profitability to vertebrates, particularly in the case of highly mobile taxa such as bats (Ewert et al., 2023). By relating bat activity levels to land cover composition in one of the best preserved dry grassland hotspot in the Mediterranean, our work highlights a key role of high diversity grasslands – as listed in the Habitats Directive – in sustaining bat populations.

In our study system, richer bat assemblages and higher overall activity levels occurred at sites characterized by more diverse land cover mosaics, a result in line with the multi-habitat specialization of most bats, that may require different habitat types to completely fulfill their ecological needs and thus select for more diversified landscapes (Ducci et al., 2015; Laforge et al., 2021). Besides, the availability of sloping terrain also fostered higher bat activity, together with closer distances to caves. These two factors are strongly related in our study area, where sloping terrain is usually associated to rocky ravines and gorges ("*gravine*", in Italian), whose peculiar mesoclimatic conditions (e.g., higher humidity, air circulation patterns) and linear geomorphology may represent to bats either profitable foraging opportunities by increasing insect availability, or favored commuting routes, respectively (O'Mara et al., 2021), beside often hosting complex cave systems as typical of karst landscapes, important as bat roosts (Furey and Racey, 2016). As such, the maintenance of locally richer mosaics of land cover types, and the preservation of linear elements that may enhance landscape diversity and provide diverse ecological conditions represent a key asset to environmental management of grassland habitats, particularly in protected areas (Ducci et al., 2019).

We documented the use of dry grasslands by all the bat species occurring in our study area, including some of conservation concern and listed as priority species within the EU legislation. Besides, and in contrast to other work from more forested areas (e.g., Kusch et al., 2004; Russ and Montgomery, 2002), the activity levels we recorded at grassland sites were comparable to those in woodland ones, suggesting that the same habitat types may differ in their importance to species in different ecological and geographical contexts, possibly due to species' adaptation to local conditions (Ancillotto et al., 2015a,b). The unique landscape where we conducted our work may have also influenced the relationship between eco-

Table 2
Effect of land cover composition and landscape features on bats in the open environments (n = 35) within the Alta Murgia National Park, southern Italy. Significant effects are evidenced in *italics*. SE = Standard Error.

Predictors	Total activity		α diversity		Open/edge space foragers		Narrow space foragers	
	Estimate ± SE	p	Estimate ± SE	p	Estimate ± SE	p	Estimate ± SE	p
Distance to closest cave	−0.010 ± 0.001	*<0.001*	0.012 ± 0.001	0.449	0.000 ± 0.001	0.183	−0.308 ± 0.001	*<0.001*
Grassland (%)	−0.046 ± 0.020	0.961	0.038 ± 0.020	0.366	0.037 ± 0.011	0.160	0.091 ± 0.010	*0.003*
HDG (%)	0.019 ± 0.001	*<0.001*	0.005 ± 0.003	0.178	0.033 ± 0.000	*<0.001*	0.039 ± 0.001	*<0.001*
Grassland ∗ HDG	0.002 ± 0.005	0.089	0.000 ± 0.010	0.345	0.022 ± 0.021	0.175	−0.015 ± 0.000	*<0.001*
Woodland (%)	0.008 ± 0.002	0.150	0.016 ± 0.011	0.156	0.051 ± 0.001	*0.003*	−0.008 ± 0.000	*0.009*
Cropland (%)	0.018 ± 0.009	0.232	0.013 ± 0.201	0.292	0.029 ± 0.008	0.126	−0.059 ± 0.001	*0.047*
Land Cover Diversity	0.007 ± 0.000	*<0.001*	0.817 ± 0.003	*0.024*	0.814 ± 0.090	0.096	0.183 ± 0.030	0.764
High Slope Terrain (%)	1.844 ± 0.021	*<0.001*	0.013 ± 0.002	0.082	0.020 ± 0.011	0.168	−0.009 ± 0.001	0.288
Date	0.033 ± 0.07	0.087	0.056 ± 0.011	0.078	0.450 ± 0.051	0.187	0.111 ± 0.098	0.301
R^2	0.90		0.73		0.87		0.95	

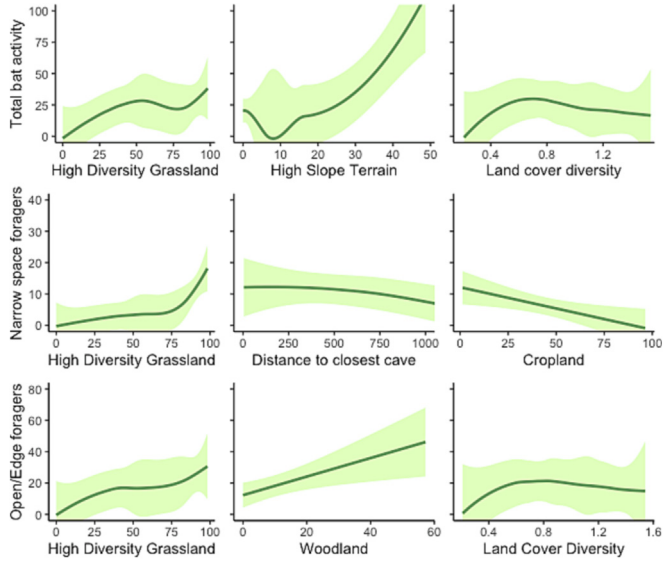

Fig. 3. Relationships between bat activity, quantified as minutes of recorded echolocation calls, and landscape composition and features, assessed at 35 grassland sites at the Alta Murgia National Park, southern Italy. Light green shaded areas indicate 95 % confidence intervals around raw data.

morphological guilds and the presence of other habitat types in the area (Ducci et al., 2015). In fact, we detected diverging effects of woodland cover upon the presence of narrow space foragers and open/edge foragers, which were negatively and positively influenced by the amounts of woodland, respectively. This result may sound counterintuitive, since narrow space foragers are usually associated with forest habitats in other ecological and geographical contexts (Treitler et al., 2016). Nonetheless, species composition of local bat assemblages in Alta Murgia, and of narrow space foragers in particular, is characterized by a set of species, namely *Myotis blythii*, *Plecotus austriacus* and *Rhinolophus ferrumequinum*, that prefer to forage over well-conserved open habitats, where they prey upon grassland-associated insects such as orthopterans, dung beetles, and several species of moths (Anderson et al., 2020; Arlettaz et al., 1997; Starik et al., 2021). This is also in agreement with the negative effect we found by cropland, specifically upon this bat guild. Besides, HDGs strongly characterize the landscape of Alta Murgia, and their rich assemblages of herbaceous vegetation – a typical feature of all the considered HD-listed habitats – actually provide a relatively complex 3-dimensional environment, suitable to narrow space foragers, e.g. in comparison to simplified monoculture cropland (Batáry et al., 2010), which may explain the preference for such habitats by bats. Higher complexity in grassland 3-dimensional vegetation structure also supports well-structured and richer insect communities, as in the case of orthopterans in Alta Murgia HDGs (Labadessa et al., 2015), therefore indirectly supporting bat habitat preferences. Conversely, the presence of wooded cover contributes to increase the availability of ecotonal margins, a key landscape element to several open/edge foraging bats recorded in farmlands, e.g. *Eptesicus serotinus, Miniopterus schreibersii* and *P. pipistrellus* (Blary et al., 2021; McHugh et al., 2019; Vincent et al., 2011). We also evidenced an interactive effect between grassland cover and the percent of HDG in shaping site attractiveness to narrow space foragers, i.e. higher amounts of HDG significantly increased their importance to these bats at smaller extents of grassland cover. This result highlights the importance of natural and semi-natural grassland in modified areas, identifying even small remnants in highly modified landscapes as a priority to conservation, as also evidenced in more fragmented grassland areas (Broken-Brow et al., 2019; Ewert et al., 2023; Ríos et al., 2022).

Land use intensification is known to alter wildlife assemblages, usually homogenizing and simplifying communities by filtering out specialized taxa (e.g., Guariento et al., 2022). From a community point of view, the composition of bat assemblages in our study area mainly shifted along a gradient of decreasing naturalness. Specifically, sites mostly comprising well-conserved high-diversity grassland were characterized by conspicuous activity levels of taxa specialized in foraging over semi-open habitats such as large *Myotis* and horseshoe bats. Conversely, sites heavily dominated by intensive cropland featured higher presence of opportunistic species such as *P. kuhlii*, which was also the only species recorded at two sites

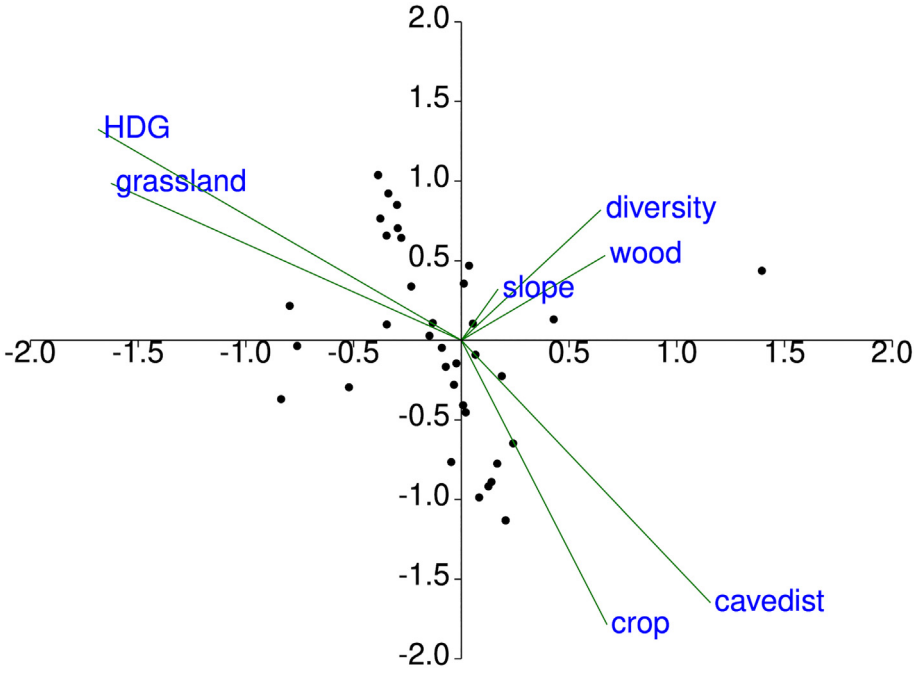

Fig. 4. Multivariate distribution of acoustic sampling sites (n = 35) by Canonical Correspondence Analysis on bat assemblage composition according to environmental descriptors within 500 m around each site, from the Alta Murgia National Park (southern Italy); cavedist = distance to closest cave; crop = percent amount of cropland; wood = percent amount of wooded vegetation; diversity = land cover Shannon diversity; grassland = percent amount of grassland; HDG = percent amount of grasslands classified as high diversity grasslands. Green vectors indicate strength and direction of each environmental descriptor in influencing assemblage composition.

comprising only cropland in their surroundings. The latter is an exceptionally plastic species, widespread across anthropogenic habitats in Mediterranean Europe such as cities and farmland (Ancillotto et al., 2016; Ancillotto et al., 2015a,b), where it is supposed to provide quantitatively relevant ecosystem services as crop protection by insect pest suppression (Russo et al., 2018). The use of cropland by grassland-adapted species as surrogate or complementary grassland-like habitat is well known among birds (Gamero et al., 2017), yet only occurs in a subset of all those species adapted to open environments, i.e. cropland actually impoverishes grassland communities by filtering out more sensitive species (Puga-Caballero et al., 2014), as we also evidenced for bats in our study. These "losers", in terms of adaptability to the replacement of grasslands with intensive cropland, are namely those considered as priority to conservation at the EU level, as in the case of many of the bat species we found in HDG-rich sites - or in Annex 1 of the EU Birds Directive (e.g., *Tetrax tetrax* and *Burhinus oedicnemus*: Sanz-Pérez et al., 2019).

5. Conclusions

Our results indicate a strong and positive relationship between bats from all the considered functional guilds and Mediterranean dry grasslands, and particularly highlight the value of high diversity grasslands listed within the EU Habitats Directive as valuable resources to foraging bats. The role of protected habitats in conserving biodiversity is obvious for plant species, as well as for the insects that depend upon them e.g. as host plants (Labadessa et al., 2021; Labadessa and Ancillotto, 2023), yet we disclose that the effects of these priority habitats may extend also onto highly mobile species such as bats (Ewert et al., 2023) and possibly several other taxa. We also revealed the combined effects of landscape composition, habitat quality and terrain structure, shedding light on the importance of considering drivers of ecological factors as well as their interactions. We finally highlight the need of more in-depth studies on the ecological role of high diversity grasslands in sustaining biodiversity as a whole, e.g. by adopting multi-taxonomic and trophic-networks approaches, particularly in highly fragmented ecosystems.

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CRediT authorship contribution statement

Leonardo Ancillotto: Conceptualization, Methodology, Investigation; Formal analysis, Writing – Original Draft, Writing – Review & Editing; **Rocco Labadessa**: Conceptualization; Methodology; Investigation; Original Draft, Writing – Review & Editing; **Federica Roscioni**: Methodology, Original Draft, Writing – Review & Editing; **Francesca Montioni**: Conceptualization, Methodology, Funding acquisition, Project Administration; **Egidio Fulco**: Investigation; **Luciana Zollo**: Funding acquisition, Supervision; **Cristiano Spilinga**: Conceptualization, Funding acquisition, Supervision, Project administration.

Data availability

Data will be made available on request.

Declaration of competing interest

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.

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