Biological Conservation 311 (2025) 111409

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Management, topography and landscape contribute to shape bird communities in Alpine semi-natural grasslands☆

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ARTICLE INFO

Keywords:
agricultural intensification
conservation
ecosystem services
farming practices
functional groups
grassland specialists

ABSTRACT

Grasslands are key habitats for biodiversity in Europe but are declining and degrading due to abandonment, conversion and intensification. Many grassland specialist species have declined; some have found refuges from intensification in mountain grasslands but are now threatened there by land use and climate changes. We assessed the link between grassland breeding bird communities (species richness and abundance of functional groups), and landscape/topography/management in 166 transects in the Italian Alps, along environmental and management gradients, using multi-model inference. All types of predictors contributed to shaping all traits of avian communities (112 species), but with varying importance. The most relevant management variable was (intensive) valley floor grasslands, influencing negatively insectivores, and positively granivorous and pest species. Among subsidies related to the Common Agricultural Policy, only late mowing (10.1.1) and organic management entered few models with positive effects. Landscape features were the most frequent predictors. Broadleaved forests influenced positively vegetation-dwelling insectivores, and negatively the number of grassland species and both ground-dwelling insectivores and granivorous species. Apple orchards negatively impacted on species richness and insectivores. Alpine grasslands affected positively grassland species, and negatively other community metrics. Finally, the number of grassland species and grassland-dwelling insectivores increased with elevation, contrary to most of other species. Future policies should revise subsidies to implement a more biodiversity-oriented management, together with the preservation of low-intensity grasslands. Preserving ecologically functional grassland only at high elevation is not enough to conserve biodiversity and related ecosystem services, due to the linkage with low elevation of many functional groups and species.

1. Introduction

Grasslands are among the most widespread and important biomes, covering more than 40 % of the Earth's land surface (FAO, 2006), and occupy 35 % of the utilised agricultural area in Europe (Smit et al., 2008). Several European grasslands are represented by semi-natural habitats, ecosystems dominated by native plant species and shaped by geophysical and biotic processes (Dixon et al., 2014) but created by human intervention to sustain livestock and maintained by mowing and/or grazing. These secondary grasslands, which have a millenarian history in the continent, are among the most iconic and biodiversity-richest habitats in Europe, playing a pivotal role for biological conservation (Petermann and Buzhdygan, 2021).

Indeed, despite the anthropogenic origin and inextricable connection with rural activities, secondary grasslands represent key habitats for many animal (Nagy, 2009; van Swaay et al., 2006) and plant species (Prangel et al., 2024; Wilhalm, 2018; Wilson et al., 2012), and contribute to characterise the identity and attractiveness of many cultural landscapes (Bengtsson et al., 2005; Eriksson and Cousins, 2014; Janišová et al., 2021; Nowak-Olejnik et al., 2020; Wang et al., 2024). In

☆ This article is part of a Special issue entitled: 'Palaearctic grasslands' published in Biological Conservation.

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https://doi.org/10.1016/j.biocon.2025.111409
Received 15 January 2025; Received in revised form 15 May 2025; Accepted 1 August 2025
Available online 8 August 2025

the last decades, many grasslands have disappeared, and the grassland share declined from 1990 to 2018 in most of European countries (Pazúr et al., 2024). Such decline can be attributed to the conversion of secondary grasslands into more remunerative crops, and to their abandonment, especially in less accessible or marginal areas (Laiolo et al., 2004; Öckinger et al., 2006; Valkó et al., 2018). The remaining ones have frequently undergone a process of severe intensification, with increased chemical inputs and mechanization (Gossner et al., 2016; Hilpold et al., 2018; Manning et al., 2015).

All those changes in grassland ecosystems across Europe are linked to socio-economic drivers, and have been influenced by the Common Agricultural Policy (CAP) and its reforms in the European Union (Barral and Detang-Dessendre, 2023; "CAP 2023-27 - European Commission", 2025; Langlais, 2023), often with unintended negative consequences for biodiversity (Marino et al., 2014). For instance, the CAP's structure and especially its subsidy mechanisms have inadvertently favoured agricultural intensification and homogenization by promoting overgrazing in semi-natural grasslands (Kindvall et al., 2022), excluding ecologically valuable pastures from receiving subsidies (Rodríguez-Rigueiro et al., 2021), and applying greening measures in grasslands too generalized to bring effective results at a local scale (Hristov et al., 2020).

These factors, altogether, have led to dramatic consequences for grassland biodiversity (Habel et al., 2019). In mountain areas like the Alpine valleys, agricultural intensification and land use changes have led to a fragmented landscape, where the persisting grasslands are often small and isolated (Cousins and Lindborg, 2008; Ríos et al., 2022). Nonetheless, these grassland remnants have a major ecological role and are crucial for biodiversity as they can act as refuges for open-habitat species that have been wiped out in the lowlands by the intensification of agricultural practices (Archaux, 2010). Furthermore, they supply (or contribute to) key ecosystem services, such as carbon sequestration, climate and water regulation (O'Mara, 2012) and can serve as source habitats for restoration and conservation interventions (Lengyel et al., 2012; Pavlacky Jr. et al., 2022). However, the unfavourable trajectories of European grasslands are particularly pronounced in mountains, and the important functions of mountain grassland remnants are jeopardised by the still ongoing decline and degradation. Land abandonment, triggered by mountain depopulation and the disappearance of local and traditional agriculture, causes dramatic landscape changes due to tree and shrub encroachment, ultimately leading to reforestation (Anthelme et al., 2003; Didier, 2001). Land conversion, linked either to the highest remuneration provided to farmers by more intensive crops (such as orchards and vineyards) or to the development of urban or industrial sites, determines the disappearance of those semi-natural habitats (Barnes et al., 2024; Stephens et al., 2008). Farming intensification, even if not leading to a complete replacement of secondary grassland, results in a drastic degradation of their ecological roles, altering communities, which often become dominated by one or a few plant species tolerant to high fertilization and frequent mowing, and disrupting ecological interactions and nutrient cycles (Oenema and Oenema, 2021). As a consequence, the role of grasslands as potential refuges for farmland biodiversity has been halted by such unfavourable changes (Korner et al., 2018). The conversion of mountain grasslands into croplands, their intensification and abandonment continue to reduce their ecological potential in many regions (Aune et al., 2018; Durán et al., 2020; Lessard-Therrien et al., 2018). Among the organisms most impacted by the changes occurred in European grasslands over recent decades, birds have been frequently used to investigate the consequences of land use and management intensification of open landscapes (Anderle et al., 2024; Padoa-Schioppa et al., 2006). Birds are indeed good indicators, sensitive to environmental changes, and act as good surrogates for more general patterns of biodiversity in mountain farmed contexts (Anderle et al., 2024). Many grassland bird species and communities have undergone progressive decline and impoverishment (Douglas et al., 2023), and such dynamics have been particularly pronounced in recent years in many European mountain areas, due to both environmental and climate changes (Bani et al., 2019; Brambilla et al., 2020; Lehikoinen et al., 2019). As a result, grassland birds are among the avian groups showing the less favourable conservation status in large parts of Europe (Gamero et al., 2017). This is very evident in Italy (Gustin et al., 2019), where the mountain grassland indicator shows a negative trend (Rete Rurale Nazionale and Lipu, 2023) despite the inclusion of some generalist and increasing species, like the black redstart (*Phoenicurus ochruros*). Land abandonment and farming intensification indeed are dramatically impacting on many species and communities in Alpine valleys (Assandri et al., 2019a).

The negative effects of grassland loss and degradation on birds imply cascading consequences on ecosystem processes and functions. In many farmed environments (with grasslands making no exception), birds indeed play fundamental functions, spanning from seed dispersal (Garcia et al., 2010; Heleno et al., 2011) to pest control (Roseo et al., 2024) and cultural services (Brambilla and Ronchi, 2020; Zielonka et al., 2024). Functionally diverse and rich bird communities are therefore important for farm management, sustainability and productivity, limiting losses and the need for chemicals, and enhancing farm multifunctionality (Díaz-Siefer et al., 2022; Teuscher et al., 2015).

With this work, we assess the link between bird communities, landscape features, and agricultural types in mountain grasslands in the Italian Alps (Fig. 1), where the effects of ongoing transformations are particularly evident (Assandri et al., 2019a; Brambilla, 2020). Mountain grassland birds are affected by management practices (e.g., Shaffer et al., 2025), local topography and climate and their relative interactions (Assandri et al., 2019b; Brambilla et al., 2020; Martin-Sirito et al., 2025). Management practices supported by EU agricultural subsidies within the CAP framework are particularly relevant for grassland species (e.g., Andreatta et al., 2025), as they are often implemented over large shares of the European agroecosystems. Evaluating the effects of these main drivers on birds, considering both communities and functional groups, is key to the development of conservation measures for avian biodiversity and for ecosystems as well. Effective strategies are needed to halt and reverse the current dramatic trend of farmland birds, which is indeed of utmost importance both for conservation (Dotta et al., 2016; Pavlacky Jr. et al., 2022; Vickery et al., 2000) and for harnessing benefits delivered by wild birds to increase the sustainability of modern agriculture (e.g. Roseo et al., 2024).

With this work, we specifically focus on bird species richness, richness of grassland specialists, and on the abundance of different functional groups of birds. We consider groups of species involved in the delivery of key ecosystem services and of potential disservices in agricultural landscapes. Particular attention was given to insectivore species, because of their key role for farmed areas (Nyffeler et al., 2018; Díaz-Siefer et al., 2022), granivores, who could contribute to weed control, and diurnal raptors, which are important for the predation pressure they may exert on rodents.

2. Materials and methods

2.1. Study area

The study was carried out in grassland-dominated areas within the Alpine region, in the Trento province (north-eastern Italy; coordinates 45.67–46.51° N and 10.51–11.96° E). This is a mountainous region (elevation range: 65–3764 m asl) with a temperate climate in the lowland areas, gradually transitioning into a cold alpine climate at higher elevation. Annual rainfall is mostly comprised within the range of 700–1500 mm. Nearly half of the region is covered by woodland, and grasslands (which comprise secondary habitats such as hay meadows and pastures, and primary alpine grassland at high elevation), are generally found interspersed within a matrix dominated by woodland, other crops (especially orchards and vineyards) and urban areas. Secondary grasslands are located approximately between 250 m and 2000 m asl, while alpine grasslands are mostly found above such elevation

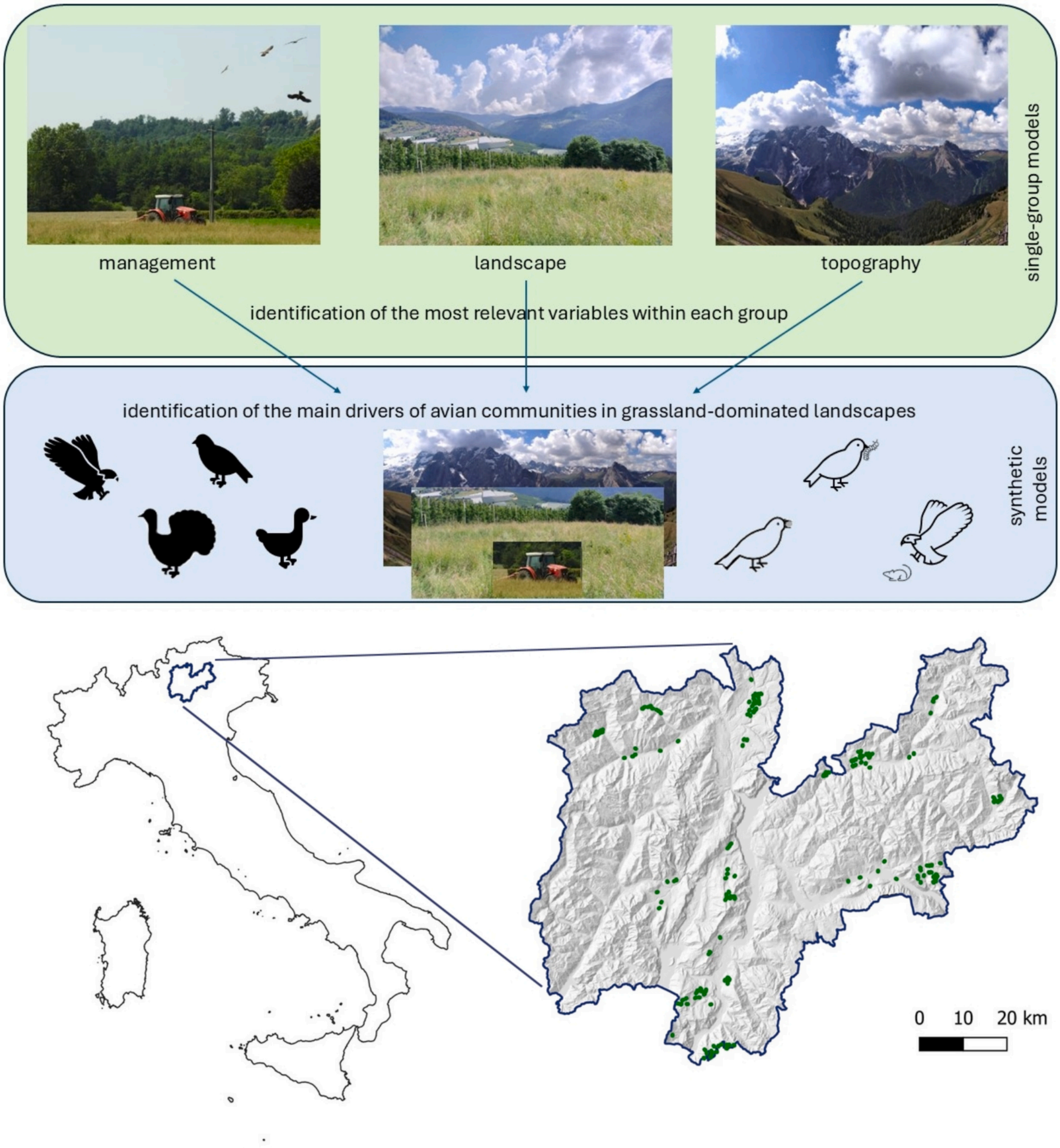

Fig. 1. Schematic representation of the drivers of mountain grassland bird communities in the Alps assessed in the study, and location of the study area (Trento province within Italy, and linear transects shown in green within the Trento province). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and up to c. 2600–2700 m asl (depending on the context). Within this study, we focussed on secondary grasslands, i.e. i) hay meadows, usually mown 1–4 times per year (Assandri et al., 2019a), and ii) pastures and alpine grasslands anthropogenically expanded towards lower elevation to increase the extent of grazed areas, below the treeline. Within this elevation belt, grasslands have been created and maintained by human activities. Grasslands have dramatically declined in the Trento province in recent decades (Provincia Autonoma di Trento, 2017), as well as in many other Alpine regions (Marini et al., 2011; Niedrist et al., 2009) and in Europe in general (see above).

Within this context, grassland birds have been surveyed along 166 linear transects (length: 200 m) scattered within 18 areas corresponding to the main grassland extents of the province and representing the environmental and management gradients of grassland systems in the area, based on elevational gradients and previous knowledge on the distribution of low- and high-intensity hay meadows (Assandri et al., 2019a). Transects overlaid hay meadows and pastures at different elevation (from 300 to 1700 m asl), and were placed over existing paths, tracks or low-traffic unpaved roads.

2.2. Fieldwork

Transects were surveyed twice per year between May and June, in the early morning, from dawn to c. 10–11 a.m., depending on the daily weather, and recording all contacts with any bird species within a 100 m-belt from the transect (i.e., covering a 7.14-ha extent). Such a survey method is particularly suited for investigating the ecology of passerines and other small to medium-sized birds in grasslands and other farmed open and semi-open environments (Assandri et al., 2019b; Assandri et al., 2019a; Brambilla et al., 2024). In a few cases, transects were surveyed three times per year (adding a further visit in late June–July, depending on elevation). Seventy-six transects were surveyed in one year, 36 in two years, 48 in three years, and nine in four years, between 2014 and 2019. We considered the overall outcomes of bird surveys but taking into account the different sampling efforts (see under Analyses).

2.3. Environmental predictors

The environmental predictors considered represent the three groups of possible drivers identified on the basis of the known ecological relationships between grassland birds and the environments they inhabit (Brambilla et al., 2020; Anderle et al., 2022). We therefore focussed on: i) topographical variables, considering average elevation of the transect (which, at the study scale, represents the main climate variations) and the elevation range within the transect, describing average slope and expected general habitat and microclimate heterogeneity within the buffer (Rogora et al., 2019; Sabatini et al., 2018); ii) landscape variables, focussing on landscape composition, i.e. land-use/land-cover (LULC), considering the proportional cover of natural, semi-natural and anthropogenic habitats (Canonne et al., 2024); and iii) management variables, which are particularly relevant for agroecosystems and can have outstanding importance for structurally simple habitats like many grasslands (Shew and Nielsen, 2021). Among the latter, we focussed on variables describing measures and incentives related to the CAP, because of their relevance for large-scale policies and related conservation implications, as well as to the fine-scale actual utilisation of grassland habitats. Specifically, the management variables we considered were: i) different agro-botanical types of grassland depending on the context and general management intensity (from intensive lowland grasslands to species-rich unfertilised grasslands; La Notte, 2014; Assandri et al., 2019a). Agro-botanical grassland types have been treated under management variables and not under LULC because from a landscape perspective they are all mown grasslands); ii) use for hay making and/or for grazing, with or without other marginal elements (trees/shrubs/rocks); iii) stocking density, computed as adult livestock units (LU) per hectare (where one LU corresponds to 83 kg/year of nitrogen equivalent), which is a good indicator of fertilization level of meadows; iv) payments received from CAP subsidies. The latter include different schemes funded under different categories of subsidies: within "M10 - Agri-environment-climate", subsidies for mowing (operation 10.1.1), and subsidies for mountain pastures (10.1.2), and within "M11 - Organic farming", incentives for the introduction or the maintenance of organic management (11.1.1 and 11.2.1). Incentives for organic management were considered separately for grasslands and for other crops and have no associated prescriptions about mowing period (while the maximum LU/ha equivalent allowed is two). For details about environmental predictors, see Table 1; see also Brambilla et al. (2021) for details about the management variables.

Table 1
Variables used to evaluate the effects of different drivers on avian communities and functional groups in grassland-dominated landscapes in the Italian Alps. Variables excluded from models are those for which a statement is reported under the column "reason for exclusion".

Type of variables, variable	Units	Reason for exclusion
1. Management		
1.1 Agro-botanical type of grasslands		
Species-rich grasslands that should not be fertilized	Proportion	
Dry species-rich grasslands with little fertilization	Proportion	
Valley floor grasslands on plains or slopes <10°, excluding species-rich grassland	Proportion	
Mountainside grasslands (all other grasslands)	Proportion	
1.2 Livestock units	mean LU/ha	
1.3 Grassland utilisation		
Pastures with trees and shrubs (20 % cover of woody vegetation)	Proportion	
Pastures with trees and shrubs (50 % cover of woody vegetation)	Proportion	
Pasture	Proportion	
Pastures with rocks (rock cover 20 %)	Proportion	Too few
Pastures with rocks (rock cover 50 %)	Proportion	Too few
Grazed hay meadows	Proportion	Too few
Meadows	Proportion	
1.4 CAP subsidies (operation number)		
Subsidies for mowing (operation 10.1.1)	m^2 subsidised	
Subsidies for mountain pastures (10.1.2)	m^2 subsidised	
Incentives for introduction (11.1.1) or maintenance (11.2.1) of organic management in grasslands	m^2 subsidised	
Incentives for introduction (11.1.1) or maintenance (11.2.1) of organic management in other crops	m^2 subsidised	
Management for N2000 grasslands (additional measure within 10.1.1)	m^2 subsidised	Too few
Management for species rich grasslands (additional measure within 10.1.1)	m^2 subsidised	Too few
Compensation for mountain farming (13.1.1)	m^2 subsidised	Too collinear
2. Landscape composition		
All grasslands	Proportion	
Running waters	Proportion	
Water bodies and wetlands	Proportion	Too few
Transitional shrublands/woodlands	Proportion	
Transitional marginal areas	Proportion	
Urban areas and infrastructures	Proportion	
Coniferous forests	Proportion	
Broadleaved forests	Proportion	
Mixed forests	Proportion	
Quarries	Proportion	Too few
Hedgerows and tree lines	Proportion	
Shrubs	Proportion	
Arable crops	Proportion	
Heterogeneous crops (fine-scale crop mosaics)	Proportion	Too few
Apple orchards	Proportion	
Grazed grasslands	Proportion	
Alpine grasslands	Proportion	
Permanent hay meadows	Proportion	Too collinear
Rocks and bare soil	Proportion	Too few
Mires	Proportion	Too few
Vineyards	Proportion	Too few
3. Topography		
Mean elevation	m asl	
Elevation range (max elevation – min elevation)	m	

2.4. Analyses

We explored the effect of different predictors on variables representing i) overall avian species richness, ii) the richness of grassland specialists, and iii) the overall abundance of different functional groups of birds involved in key ecosystem services and potential disservices in agricultural landscapes. The first two variables can be used to explore the drivers of conservation values in grasslands, whereas those describing functional guilds, considering the number of individuals performing a given function, represent the potential for ecosystem services/disservices and thus are particularly important to identify strategies for leveraging on bird contribution to agriculture. For the latter analysis, we summed the individuals observed for different functional groups obtained by clustering the surveyed species into functional categories based on their diet and foraging behaviour (cf. Brambilla and Gatti, 2022), relying on existing databases and information (Cramp, 1998; Tobias et al., 2022), with minor adaptations to better fit the classification to the local context (see Table S1). The six groups were therefore: i) all functional insectivores (contributing to overall insect control), ii) functional insectivores foraging in grassland (birds foraging directly on grassland vegetation or on ground within grasslands, potentially particularly relevant for hay and fodder production), iii) insectivores foraging on vegetation canopy (excluding woodpeckers and ground-foragers; potentially particularly relevant for crops in general), iv) seed-eating species (granivores), v) raptor species, and vi) agricultural pest species (Fig. 2, Table S1). Pest species are birds that can impact on crops by eating crop seeds or fruits, and in the study area include pigeons (Columbidae, two species), thrushes (Turdidae, two species), corvids (Corvidae, five species), the Eurasian starlings (*Sturnus vulgaris*), and sparrows (Passeridae, two species).

Species occurring only as migrants within the area were excluded from all the analyses. In both the species richness estimates, we excluded raptors, herons, gulls, aerial foragers (swifts, swallows and martins), Alpine chough *Pyrrhocorax graculus*, raven *Corvus corax*, which all have territories larger than the surveyed extent around transects and/or move over larger areas. However, we retained diurnal raptors as a functional group, considering individuals observed hunting or perched within/over the transect plot.

To test the effect of topographic, management and landscape factors on the richness and abundance of bird species we run Generalized Linear Mixed Models (GLMM). For each category we run four different models: i) one including management variables, two including LULC variables, i. e. ii) all grassland types considered together, and iii) all other variables, respectively, because grassland cover led to serious multicollinearity issues when tested together with the other variables, and iv) one including topographic variables. Given that transects were surveyed between one and four years, we entered in all the models the number of years a transect was surveyed as a predictor (after evaluating that it worked better for all models than the number of individual surveys carried out at a given transect, the two being obviously almost perfectly correlated). Given that transects were somehow clustered within the 18 study areas, we used the specific area as a grouping (random) factor within the model. The full list of variables considered in each model is reported in Table 1. Variables with less than seven cases different from 0 were removed from models. Given that one variable (LU) was not available for some transects, the effective sample size for the analyses was temporarily reduced to 146. However, this variable was not included in any of the final models for the different dependent variables, so we re-run all the analyses on the full dataset and all results presented refer to the latter. Models were run in R (R Core Team, 2021), using the glmmTMB package (Brooks et al., 2017) and MuMIn (Bartoń, K., 2010).

At each step, before modelling, we tested the multicollinearity of the predictors by calculating the Variance Inflation Factor (VIF) of each predictor (“check_collinearity” function from the R package “performance”, Lüdecke et al., 2021) and removed from the models the

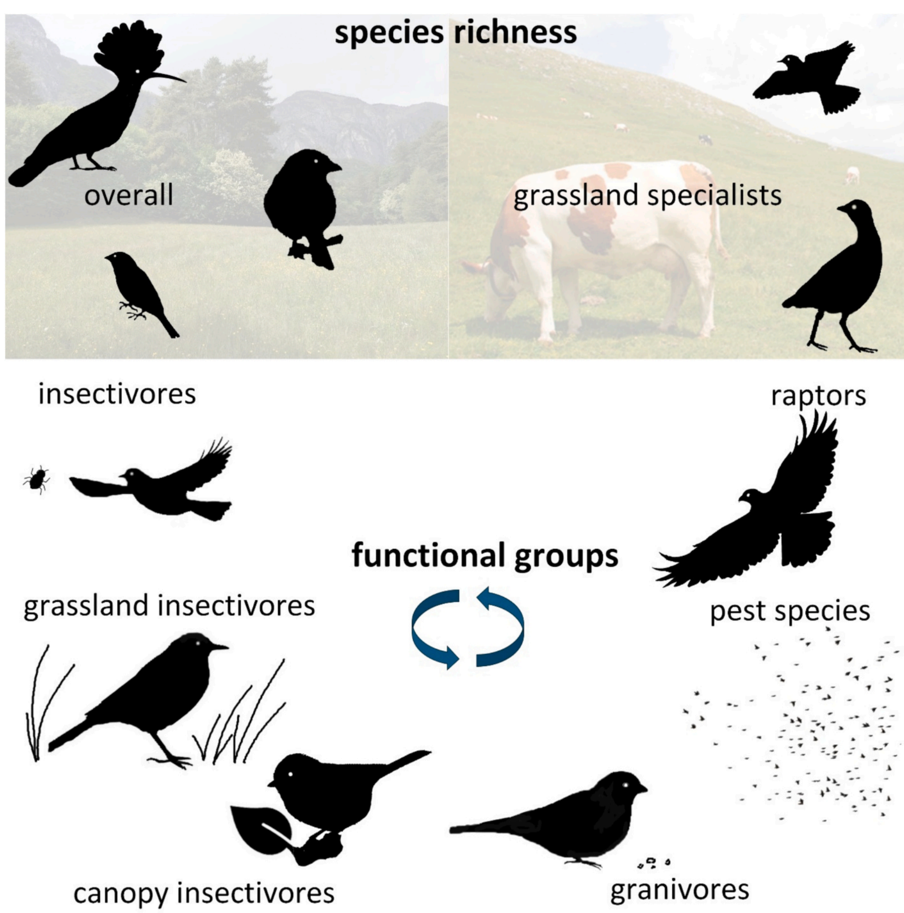

Fig. 2. Community traits and functional groups considered in the analyses.

variables with a GVIF (1 / (2 × Df)) greater than 3 (Fox and Monette, 1992). Given that the overall amount of grassland habitats was strongly correlated with all other landscape variables, leading to severe collinearity issues, it was tested alone.

Then, we scaled all predictors and built Poisson models for most group of predictors except for grassland species richness and all functional insectivores for which we performed negative binomial models due to overdispersion (models were checked for overdispersion using the dedicated command in the package "performance", Lüdecke et al., 2021; Nakagawa et al., 2017). Each model was tested for consistency with expected residual patterns, using the "DHARMa" (Hartig, 2020) commands to validate the model, by using 500 simulated residuals' distributions to assess the uniformity of the simulated vs. observed dispersion, the possible occurrence of outliers, distribution of quantile residuals and the potential occurrence of zero-inflation. All models met assumptions with the partial exception of that for species richness of grassland specialists. To evaluate the relative importance of each group of predictors, we calculated the marginal and conditional R^2 of each single-group model considering a model including only predictors with a significant ($P < 0.05$) or nearly significant ($0.05 < P < 0.1$) effect in the full model.

Then, for each dependent variables, we tested the variables showing a significant or nearly significant effect ($P < 0.1$) in the single-group models, in a final model combining the most relevant predictors belonging to each specific group of variables (and checking again multicollinearity). We compared all possible models within the resulting set of variables by means of the 'dredge' function of the "MuMin" package (Bartoń, K., 2010), computing the support according to the Akaike's Information Criterion corrected for small sample size (AICc). Then, we removed models with uninformative parameters following Arnold (2010), i.e. those that include an additional variable compared to more supported (i.e., with lower AICc) models, and selected the remaining models within ΔAICc<2. If there were more than one single supported model, we carried out a model averaging procedure. We computed the AICc and R^2 (both marginal and conditional values, to highlight the contribution of the grouping factor) for each synthetic model by fitting a model including all the variables comprised within the averaged model.

3. Results

3.1. General patterns

Overall, we recorded 112 bird species during the breeding season (Table S1). Depending on the response variable, management, landscape or topographic features were the most relevant predictors of community traits (Tables 2 and 3). In any case, all contribute to some extent in explaining the observed patterns of species richness and abundance of different functional groups: for all the metrics, the synthetic models integrated predictors from different groups and explained more variation in the data (higher R^2) than the single-group models (Table 2; the only exception being represented by diurnal raptors). Synthetic models were also more supported (lower AICc; Table 2) than the single-group models; even if the models used for computing AICc for single-group models were not necessarily the most parsimonious ones, the difference in favour of synthetic models was always too large to be attributable to those procedural differences. In the case of diurnal raptors, the final model coincided with the landscape one with the only addition of mean elevation, and the overall performance of the final synthetic model was substantially the same of the landscape one.

In most cases, models' R^2 were pretty good, also the marginal ones, suggesting that models explained a high proportion of variation in community metrics and that predictors were adequate descriptors of bird communities' drivers (Tables 2 and 3). However, conditional R^2 were larger than marginal ones for most metrics, revealing an effect of the sub-area and hence some large-scale variations in bird community not entirely explained by the drivers we considered. All coefficients (plus relative standard error) for all variables included in final models and R^2 are reported in Table 3.

3.2. The effects of grassland management on bird communities

Species-rich grasslands that should not be fertilized had a negative impact on all functional insectivores but positively affected the abundance of granivorous species. Valley floor grasslands were included in the synthetic models of many functional groups and exerted a negative influence on all functional insectivores (Fig. 3a) and canopy-dwelling insectivorous species (Fig. 3b), whereas they had a positive effect on granivorous (Fig. 3d) and pest species (Fig. 3c). Mountainside grasslands were negatively related to the abundance of diurnal raptors, while

Table 2
AICc and R^2 values for single group- and synthetic models, for each community metrics (see text for the approach used for computing such values). Within the landscape group, we reported the values for the models without the overall extent of grassland habitats, which was tested apart because of collinearity issues, and also when it significantly affected the response variable, the model with overall grassland extent showed a higher AICc and a lower R^2 than the model with the other landscape variables.

	species richness	grassland species richness	all functional insectivores	functional insectivores foraging in grassland	functional insectivores foraging on canopy	granivorous species	diurnal raptors	pest species
AICc								
Management model	1011.06	626.17	1030.07	845.46	926.31	1359.95	468.83	1574.51
Landscape model	1010.81	615.44	1092.62	871.05	971.78	1878.48	485.07	1663.10
Topographic model	1009.24	588.31	1028.78	844.14	914.09	[a]	[a]	1543.89
Final model	1012.00	585.40	1021.79	828.18	902.56	1543.4	465.16	1103.71
R^2 marginal/conditional								
Management model	0.50/0.54	0.06/0.46	0.46/0.63	0.24/0.41	0.10/0.16	0.57/0.80	0.10/0.34	0.33/0.86
Landscape model	0.45/0.55	0.18/0.38	0.076/0.54	0.18/0.51	0.09/0.68	0.10/0.68	0.07/0.37	0.19/0.89
Topographic model	0.47/0.56	0.36/0.41	0.079/0.11	0.38/0.50	0.10/0.17	[a]	[a]	0.35/0.88
Final model	0.48/0.56	0.43/0.45	0.55/0.68	0.46/0.52	0.51/0.70	0.57/0.80	0.17/0.36	0.45/0.60

[a] No variables selected within the model.

Table 3
Averaged final models (obtained through conditional averaging) for each functional group and measure of species richness. Predictors are subdivided according to their type (management, landscape, topography). R^2 was computed considering a model including all the predictors comprised within the averaged model.

Variables	Species richness	Grassland species richness	All functional insectivores	Functional insectivores foraging in grassland	Functional insectivores foraging on canopy	Granivorous species	Diurnal raptors	Pest species
Management								
Species-rich grasslands that should not be fertilized			−0.05 ± 0.03			0.05 ± 0.02		
Valley floor grasslands			−0.03 ± 0.05		−0.16 ± 0.06	0.19 ± 0.04		0.11 ± 0.10
Mountainside grasslands							−0.10 ± 0.10	
Pastures with trees and shrubs (20 %)	−0.003 ± 0.01		−0.003 ± 0.01			−0.07 ± 0.03		
Pastures with trees and shrubs (50 %)			0.03 ± 0.02	0.05 ± 0.02				
Meadows								0.21 ± 0.06
CAP subsidies (operation number)								
Subsidies for mowing (10.1.1)				0.09 ± 0.03				
Organic management in grasslands						0.20 ± 0.02	0.20 ± 0.14	
Landscape composition								
Running waters								−0.03 ± 0.06
Pastures	−0.01 ± 0.02		−0.03 ± 0.03					
Transitional shrublands/ woodlands						0.09 ± 0.02		
Urban areas and infrastructures							−0.20 ± 0.14	0.18 ± 0.06
Coniferous forests					0.08 ± 0.03			
Broadleaved forests		−0.18 ± 0.07		−0.11 ± 0.04	0.07 ± 0.03	−0.07 ± 0.03		
Mixed forests					0.03 ± 0.02			
Shrubs				0.05 ± 0.02				
Apple orchards	−0.004 ± 0.01		−0.07 ± 0.05	−0.04 ± 0.06				
Grazed grasslands		0.02 ± 0.04						
Alpine grasslands		0.03 ± 0.05			−0.04 ± 0.05		−0.07 ± 0.13	
Hedgerows and tree lines			0.06 ± 0.03		0.08 ± 0.03			
All grasslands							0.16 ± 0.14	
Topography								
Mean elevation	−0.01 ± 0.02	0.40 ± 0.07		0.17 ± 0.04	−0.15 ± 0.05			−0.40 ± 0.08
Elevation range	0.02 ± 0.02	−0.12 ± 0.05	0.09 ± 0.03		0.10 ± 0.04			
R2 marginal/conditional	0.48/0.56	0.43/0.45	0.55/0.68	0.46/0.52	0.51/0.70	0.57/0.80	0.17/0.36	0.45/0.60

meadows were positively related to the abundance of pest species. Pastures covered by 20 % with woody vegetation resulted in a weak but negative effect on the overall species richness and on the abundance of functional insectivores and granivorous species. Conversely, those that had a 50 % coverage of shrubs and trees were associated with a higher abundance of insectivores and specifically ground-dwelling insectivorous species. CAP subsidies were selected in a few of the final models considered. Specifically, the operation 10.1.1 (payments for mowing), had a positive influence on ground-dwelling insectivores, whilst the incentive for organic management in grasslands resulted in a positive effect on the predicted abundance of granivorous species and diurnal raptors.

3.3. *The effects of land cover and topographical predictors on grassland bird communities*

Landscape (LULC) features were the most frequently included predictors in the final models. Among these, the most selected (at least for half of the response variables) were broadleaved forests, apple orchards, and alpine grasslands. The former had a positive influence on the abundance of canopy-dwelling insectivorous species (Fig. 4b) but had a strong negative impact on the number of grassland species (Fig. 4a), and on the abundance of ground-dwelling insectivores (Fig. 4d), and also negatively affected granivorous species (Fig. 4d). Apple orchards had a negative impact on all the metrics for which they were included in the final model, affecting the number of species (Fig. 5a), and the abundance of all functional insectivores (Fig. 5b), as well as grassland-dwelling insectivorous species (Fig. 5c). The proportion covered by alpine grasslands was negatively related to the predicted abundance of canopy-dwelling insectivores (Fig. 6b) and diurnal raptors (Fig. 6c), but had a positive effect on the number of grassland species (Fig. 6a).

The other landscape variables were included with lower frequency within the final models. Running waters influenced negatively the abundance of pest species. The proportion of pastures was negatively related to the number of species and to the predicted abundance of all functional insectivores. Transitional shrublands and woodlands only

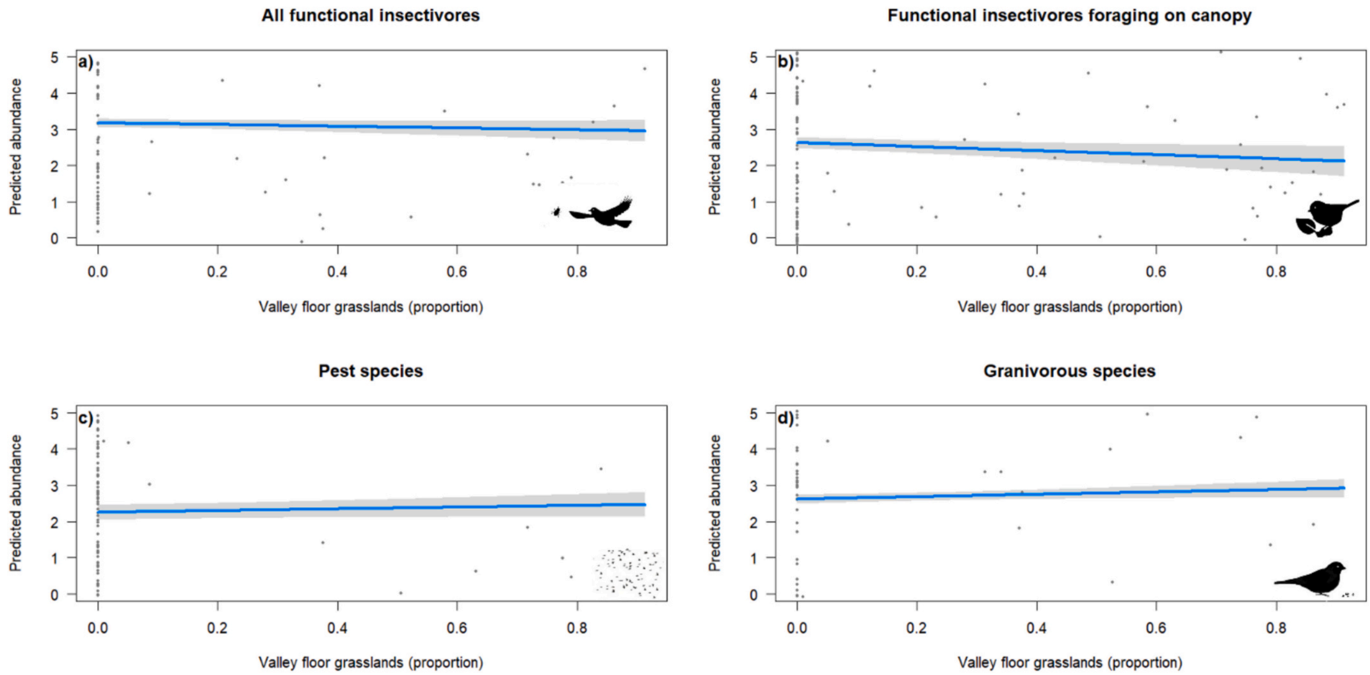

Fig. 3. Predicted abundance of a) all functional insectivores, b) functional insectivores foraging on canopy, c) pest species and d) granivorous species in relation to the proportional cover of valley floor grasslands.

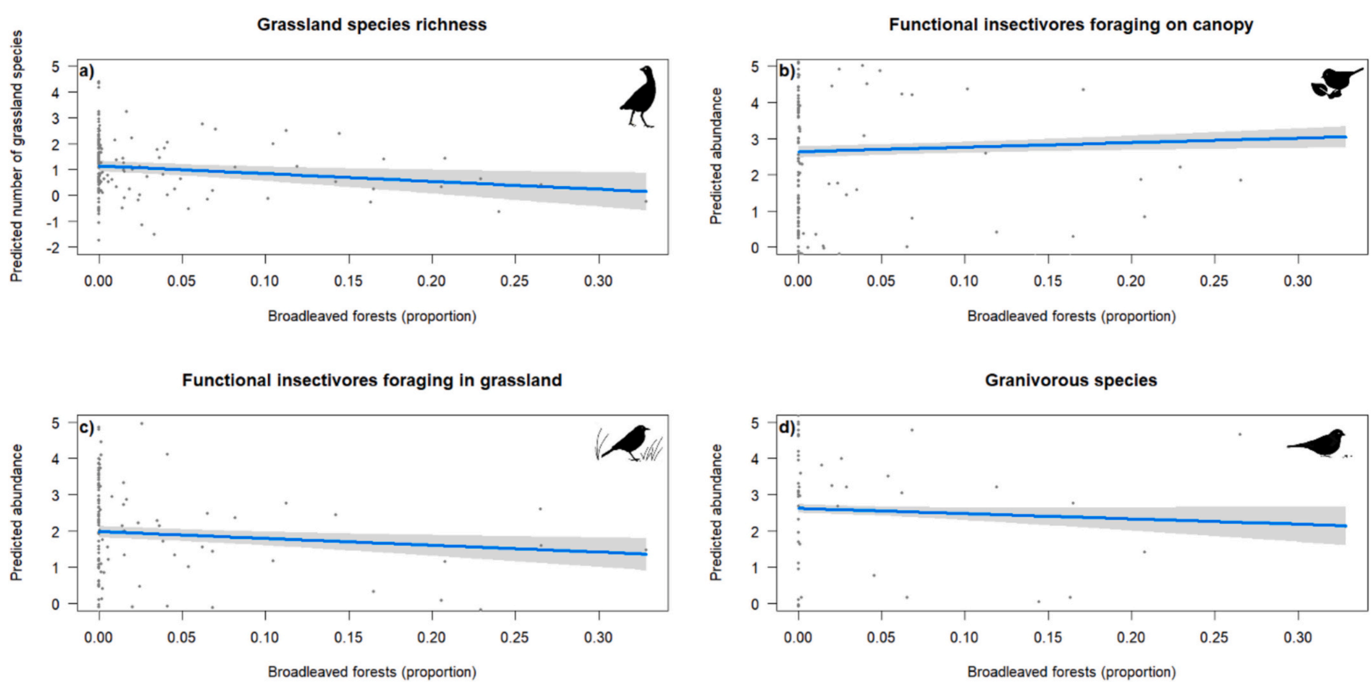

Fig. 4. Predicted a) number of grassland species, and abundance of b) functional insectivores foraging on canopy, c) functional insectivores foraging in grassland, and d) granivorous species in relation to the proportional cover of broadleaved forests.

had a weak positive impact on granivorous species, while shrubs positively influenced the abundance of ground-dwelling insectivores. Hedgerows and tree lines positively predicted the abundance of all functional insectivores and canopy-dwelling insectivores. The abundance of diurnal raptors diminished with the increasing extent of urban areas and infrastructures, conversely to what occurs with pest species.

Similarly to broadleaved forests, coniferous and mixed forests had a positive influence on canopy-dwelling insectivorous species. Grazed grasslands had a positive effect on the number of grassland species, while all grasslands had a positive influence on the abundance of diurnal raptors. Finally, the number of grassland species and the abundance of grassland-dwelling insectivorous species increased with increasing mean elevation, contrary to species richness and the abundance of canopy-dwelling insectivores, and pest species. The elevation range had a negative impact on grassland species richness, but had a positive effect on the overall species richness and on the abundance of all insectivores and canopy-dwelling insectivores.

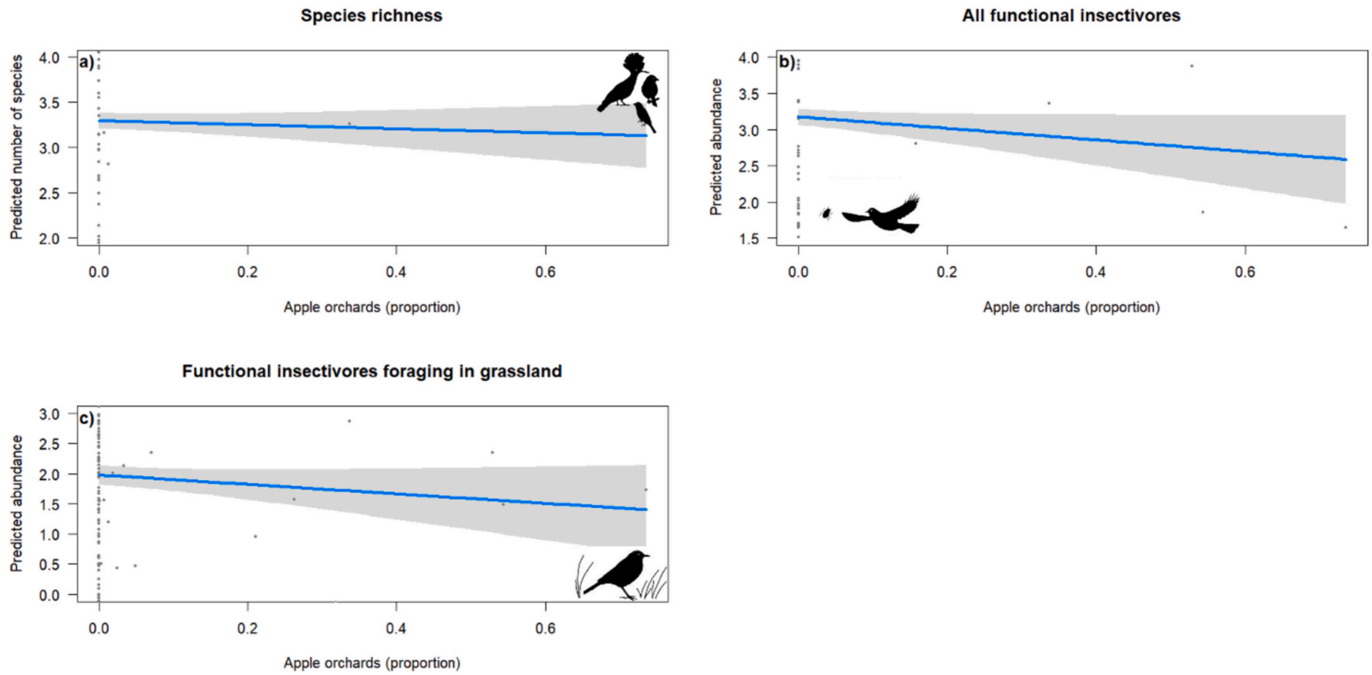

Fig. 5. Predicted a) number of species and abundance of b) all functional insectivores, and c) functional insectivores foraging in grasslands in relation to the proportional cover of apple orchards.

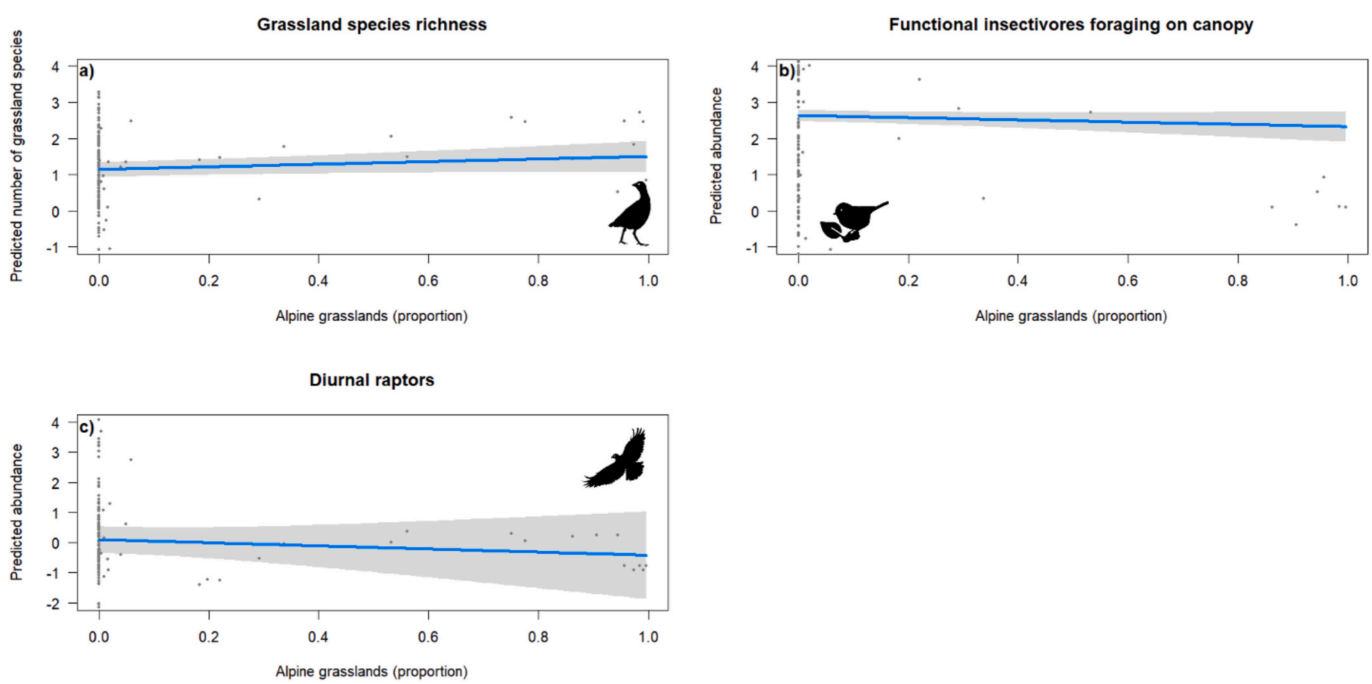

Fig. 6. Predicted a) number of grassland species, and abundance of b) functional insectivores foraging on canopy and c) diurnal raptors in relation to the proportional cover of alpine grasslands.

4. Discussion

Semi-natural grasslands are one of the richest habitats in terms of biodiversity throughout Europe (Pykälä, 2000; Veen et al., 2014). The high number of bird species found during the breeding season along transects located in the Italian Alps confirmed the importance of semi-natural grasslands for biodiversity, despite the recent ecological degradation they underwent in many European and Alpine areas (Archaux, 2007; Assandri et al., 2019b; Brambilla et al., 2021; Korner et al., 2018), including the study region (Assandri et al., 2019b; Brambilla et al., 2021).

On the one hand, our work showed that breeding bird communities in grassland-dominated landscapes are shaped by the concomitant effect of abiotic factors (topography, and in particular elevation and the associated climatic variation), landscape characteristics and management practices. This is consistent with previous studies on grassland avian communities in the same (Assandri et al., 2019a) and other mountain regions (Brambilla and Ronchi, 2020). On the other hand, the links between some metrics and drivers like elevation and agro-botanical type of grassland reflect the consequences of degradation trend experienced by grasslands in the study region on bird species and communities (Assandri et al., 2019b; Brambilla and Pedrini, 2013).

4.1. Topography

Even if most of the grassland and farmland birds observed in our study are mainly tied to lowland and low- to mid-elevation areas, elevation had a positive effect on grassland species richness (Fig. 7b) and on the abundance of grassland-foraging insectivores (Fig. 7c). This positive effect of elevation is likely due more to the higher level of intensification experienced by low-elevation grasslands, than to the occurrence of mountain species at highest sites not found at lower elevations. Intensification and grassland degradation are more severe at lower elevation (Assandri et al., 2019a), 'forcing' low-elevation species to occupy higher sites to escape the harsher impacts (Brambilla et al., 2021), leading to an increase in grassland species with elevation within the belt we considered (up to c. 1700 m asl). Furthermore, lowland grasslands are on average mown earlier and more frequently during the season compared to grasslands at higher elevations. This poses a threat to ground-nesting birds, resulting in high rates of nest losses, leading to their disappearance at low elevations (Andreatta et al., 2025). On the other side, the negative effect of elevation on other groups is perfectly consistent with the decreasing richness and abundance of most groups with increasing elevation, commonly found in the study area (Pedrini et al., 2005), Italy (Lardelli et al., 2022) and elsewhere (McCain, 2009; McCain and Grytnes, 2010). In contrast, elevation range shows the opposite pattern, with generally positive effects but a negative influence on grassland specialists. Higher elevation range can generally be linked to a greater variability, supporting a wider range of habitats and a higher species richness (Davies et al., 2007; Hortal et al., 2013; Martin et al., 2021). Nevertheless, the resulting mosaic of habitats is often associated with reduction and/or fragmentation of open environments, leading to the negative effect on grassland species we found (see also Vickery et al., 2003).

4.2. Management factors

The impact of intensification indirectly suggested by the effect of elevation on community metrics was confirmed by many descriptors of grassland management included in final models for functional groups. Management factors affected only marginally species richness, but played a key role for the abundance of all functional groups, including pest species. This result confirms the relevance of management characteristics for both ecosystem services and disservices. The extent of valley floor grasslands, which are the most intensive grasslands, exerted a negative impact on insectivores (all and canopy-dwelling species; Fig. 3a, b) and a positive impact on granivores (Fig. 3d) and pest species (Fig. 3c). This pattern suggests that grassland intensification not only has an impact on conservation values (Assandri et al., 2019a), but may also affect the supply of ecosystem services, reducing insect predation (and hence the potential insect pests' control) by birds and increasing the possible weed control, but also the potential crop damages due to birds.

Subsidies related to the Common Agricultural Policy introduced in the Trento province within the Rural Development Programme in 2000, had a low impact on bird communities and only affected three functional groups. The introduction and maintenance of organic grasslands benefitted granivorous species and diurnal raptors. Organic farming has been shown to be associated with increased plant diversity (Stein-Bachinger et al., 2021), and an overall increase in biodiversity (Tuck et al., 2014), although results are often contrasting and not always clear (Bengtsson et al., 2005). Granivorous species might benefit from a richer and more abundant plant community as it most likely increases seed availability (Milesi et al., 2008) and therefore foraging opportunities within organic grasslands. Furthermore, by limiting the use of chemical inputs, organic farming can potentially reduce the exposure of raptors to pesticides (Fuentes et al., 2024), a critical aspect for their demography (Oli et al., 2023).

The subsidy for mowing (operation 10.1.1 of the Rural Development Program) aimed at rewarding farmers that mow their grasslands at least once per year. According to our results, it was positively associated with the abundance of ground-dwelling insectivores. Those birds could be favoured by the short grassland sward after moving, but if cuts are

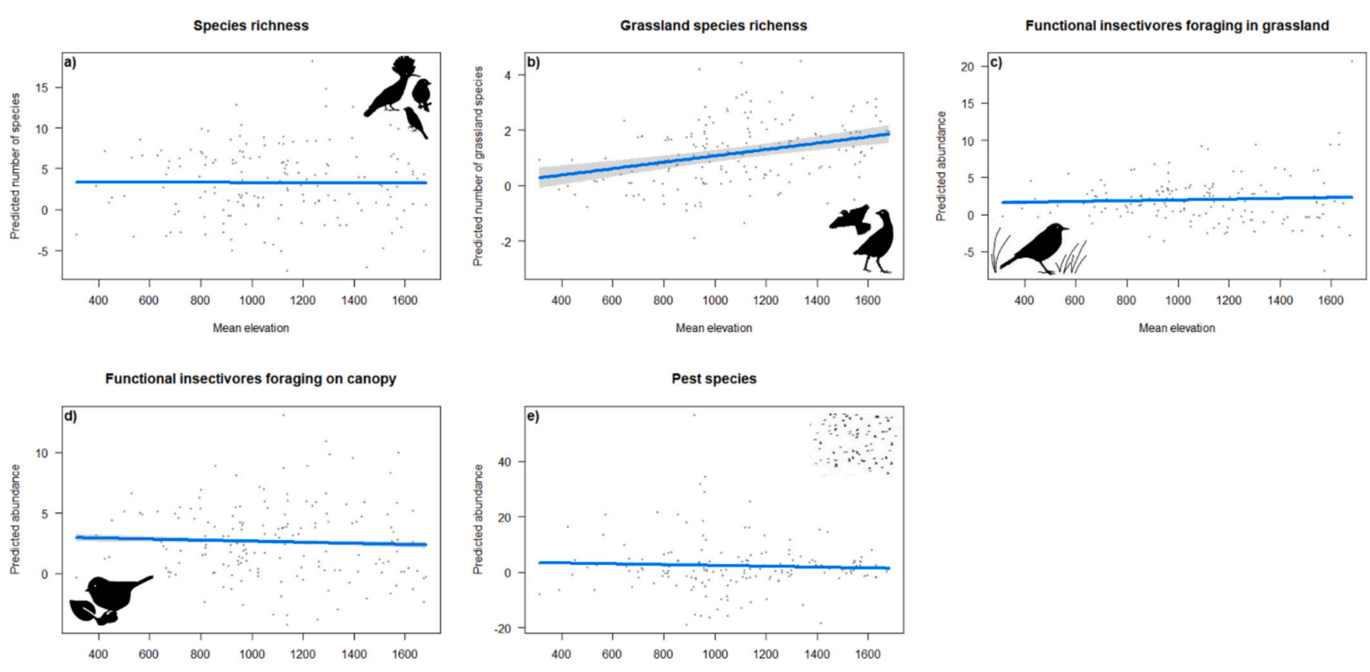

Fig. 7. Predicted a) number of species, b) number of grassland species, and abundance of c) functional insectivores foraging in grasslands, d) functional insectivores foraging on canopy, and e) pest species in relation to the mean elevation.

performed during the reproduction, they may lead to increased mortality and nest failure of ground-nesting birds (Broyer et al., 2014; Kubacka et al., 2014). This measure indeed had negative effects on the ground-nesting and grassland specialist corncrake *Crex crex* in the region (Brambilla and Pedrini, 2013; Brambilla et al., 2021). Mowing is essential not only for production purposes, but also for maintaining many ungrazed grasslands; however, the proper timing and methods of grassland cuts are crucial to ensure sustainable conditions for grassland birds (Broyer et al., 2016; Faria et al., 2016).

4.3. Landscape drivers

Landscape variables appeared important predictors for all the metrics we considered. Orchards (that in the area are mostly apple orchards), exerted a negative impact on several community metrics, likely due to the high-intensity management (see Fig. 5). Apple orchards within the province are indeed made of small trees, subject to strong mechanization and intensive farming, with abundant chemical inputs and frequent use of anti-hail nets (Brambilla et al., 2015; Granata et al., 2025). Our results confirm that the widespread conversion of former grasslands into orchards occurred in recent decades (Assandri et al., 2019a, and references therein) had profound consequences on both bird communities and the associated potential for ecosystem services, in particular the control of insect pests, given the associated decline of insectivore abundance. Considering the critical implications of insect control by vertebrate predators, such changes might potentially have important economic (Díaz-Siefer et al., 2022) and even health consequences (e.g., Frank, 2024).

Alpine grasslands had a negative effect on canopy-dwelling insectivores and diurnal raptors (Fig. 6) but positively influenced the number of grassland species (Fig. 6a). Those habitats are found on average at higher elevation than the others, characterised by harsher environmental conditions, and are occupied by species tolerant (or even adapted) to colder temperature and scarcer or more fluctuating resources (Altamirano et al., 2020; Chamberlain et al., 2016; Scott, 2011). However, they are key to some grassland specialists, like water pipit *Anthus spinoletta* and northern wheatear *Oenanthe oenanthe*, which in the Alps mostly inhabit relatively well preserved alpine grasslands (Caprio et al., 2011; Rime et al., 2024).

The negative effect of the cover of urban areas and infrastructures on the abundance of diurnal raptors is consistent with the avoidance of heavily anthropized environments by several species of birds of prey (Buxton and Benson, 2016; Eduardo et al., 2007; Tscharntke and Batáry, 2023). However, pest species were positively associated with urban settings, thus exacerbating their potential negative role for the ecosystem stability.

All forest types (broadleaved, coniferous and mixed) had a positive effect on the abundance of insectivores foraging on canopy. In addition, broadleaved forests were negatively associated with the abundance of grassland-dwelling insectivores (Fig. 4d) and of granivores (Fig. 4e), as well as with grassland species richness (Fig. 4a). The effects of broadleaved woodland on the abundance of functional insectivores and seed eating species mirror those reported from other areas (Brambilla and Gatti, 2022) and reflect the preference for open or semi-open habitats of grassland-dwelling insectivores, as expected, but also of many granivores such as buntings (Emberizidae), some finches (Fringillidae), sparrows (Passeridae), and some Phasianidae (Cramp, 1998). This means that, while forest cover may increase pest control on tree and shrub canopy, a high cover surrounding the remaining grasslands could have negative effects on other services and on the declining grassland specialists. Pastures with a low woody cover (20 %) had negative, although weak, effect on species richness and on the abundance of insectivores and granivores species, likely because the trees interrupt the continuity of the herbaceous vegetation without providing a sufficiently developed structure to support insects or offer other useful resources (Ceresa et al., 2012). At a 50 % threshold, however, tree cover appears dense enough to provide shelter, perches, and trophic resources for insectivores birds (Barbaro et al., 2014), while still maintaining open areas that are crucial for ground-dwelling species, resulting in a structurally and functionally diverse habitat (Jakobsson and Lindborg, 2017; Mendoza et al., 2014) that support insectivores according to our findings.

Similarly, the occurrence of shrubs promoted the abundance of functional insectivores foraging on grassland, while the occurrence of hedgerows and tree lines were associated with a higher abundance of all insectivores and canopy-dwelling insectivores. These landscape elements increase suitability for many insectivorous species (Brambilla and Gatti, 2022; Melo and Piratelli, 2023; Sergio et al., 2009), including conservation-priority species in the European Union (being listed in the Annex I of the Birds Directive 2009/147/EC), such as the red-backed shrike *Lanius collurio* and the barred warbler *Sylvia nisoria* (Ceresa et al., 2012; Polak, 2012). The availability of shrub and wetland cover has been reported to promote avian species richness in different farmed ecosystems, from Alpine areas (Anderle et al., 2022) to Mediterranean mosaics (Santana et al., 2025), and both these habitats can be regarded as extremely important for the conservation of bird diversity and functional roles in agroecosystems. Nonetheless, shrubs and trees may negatively impact open-habitat species (Yu et al., 2022), and well targeted strategies are needed to encompass the different requirements of open- and semi-open species in grassland landscapes (Assandri et al., 2019b).

5. Conclusion

Farming systems as well as land use shaping landscape composition should be at the core of initiatives for grassland conservation (Santana et al., 2025). Maintaining heterogeneous landscapes, with co-occurrence of grassland and forest-like environments, is crucial to support species-rich and functional avian communities in the typical grassland landscapes of the Alpine region, both in our study area and elsewhere (Anderle et al., 2023; Anderle et al., 2022; Laiolo et al., 2004). Preserving the fine-scale mosaic within and around grasslands, especially with patches of shrubs, is also needed to support grassland insectivores. The association of grassland species with higher elevation reflects the low ecological quality of grasslands found in valley floors and, more in general, at lower elevations. Within such contexts, most grasslands have undergone an extreme intensification, with high fertilization inputs and number of cuts, which led to simplified floristic composition and vegetation structure (Marini et al., 2008; Scotton et al., 2014). This degraded face of Alpine grasslands drastically reduces opportunities for insectivores, and increases suitability for pest species, potentially disrupting the functioning of those ecosystems.

Management is therefore a key component for the preservation of the ecological integrity of grasslands. Standard operations funded by the previous Rural Development Program exerted little effect on birds, and have been reported to negatively impact some ground-nesting grassland specialists. To be more effective, subsidies for biodiversity in grasslands should integrate species' requirements, taking into account mowing dates and methods (Andreatta et al., 2025; Brambilla et al., 2023; Brambilla et al., 2021; Broyer et al., 2016). Encouraging a greater participation from public authorities and a revision of subsidised practices to implement a more biodiversity-oriented management are needed and must be the aim of future policies.

CRediT authorship contribution statement

Emanuela Granata: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis. **Giacomo Assandri:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization. **Alessandro Franzoi:** Writing – review & editing, Validation, Supervision, Methodology, Investigation. **Paolo Pedrini:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Mattia Brambilla:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization, Formal analysis.

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.

Acknowledgements

This work was carried out within the project AviPAT (full name: "Progetto AviPAT - Avifauna nidificante e valutazione delle potenzialità del PSR per preservare la biodiversità degli ambienti agricoli del Trentino") and is part of EG's PhD; part of the surveys was carried out under the Life+ T.E.N. project (http://www.lifeten.tn.it/) and under Natura 2000 monitoring managed by Servizio Sviluppo Sostenibile e Aree Protette of the Trento Province. We are very grateful to F. Gubert, P. Molfetta, R. Molignoni, C. Fedrigotti for support and collaboration, and to F. Rizzolli, L. Marchesi, M. Pes, D. Scridel for contributing to the survey of some transects. Data about detailed uses of grasslands and payments/subsidies were supplied by APPAG (Agenzia Provinciale per i Pagamenti) to MUSE for the project AviPAT.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111409.

Data availability

All data used for modelling bird responses to environmental drivers are available in the open repository of Milan University at the following link https://doi.org/10.13130/RD_UNIMI/ZJ3CKD.

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