Agriculture, Ecosystems and Environment 400 (2026) 110257

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Effects of local management and landscape factors on taxonomic and functional diversity of multiple taxa in managed grasslands

Matteo Conti [a], Andrea Dalpasso [a,*], Alberto Mattia Nodari [a], Isabel Cantera [a,f], Benedetta Barzaghi [a], Mattia Brambilla [a], Andrea Ferrari [a], Gentile Francesco Ficetola [a,b], Simone Giachello [a], Elia Lo Parrino [a], Valeria Messina [a], Carlo Polidori [a], Michele Pozzi [a], Sofia Redaelli [a], Andrea Zerboni [c], Gianalberto Losapio [d,e], Mattia Falaschi [a]

[a] *Department of Environmental Science and Policy, Università degli Studi di Milano, Via Celoria 10, Milan 20133, Italy*
[b] *Univ. Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc, Laboratoire d'Écologie Alpine (LECA), Grenoble 38000, France*
[c] *Department of Earth Science "A. Desio", Università degli Studi di Milano, Via Mangiagalli 34, Milan 20133, Italy*
[d] *Department of Biosciences, Università degli Studi di Milano, Via Celoria 26, Milan 20133, Italy*
[e] *Institute of Earth Surface Dynamics (IDYST), Université de Lausanne, UNIL Mouline, Lausanne 1015, Switzerland*
[f] *Centre de Recherche en Biodiversité et Environnement (UMR5300 CRBE), CNRS, IRD, INP, UPS, Université Paul Sabatier, 31062 Toulouse, France*

ARTICLE INFO

Keywords:
Agrobiodiversity
Ecological traits
Landscape complexity
Meadows
Pollinator communities
Semi-natural habitats

ABSTRACT

Semi-natural grasslands are among the most biodiversity-rich habitats in European agroecosystems, offering a broad spectrum of resources for many species, including plants, insects, and birds, potentially increasing the provision of key ecosystem services. Grassland biodiversity can be strongly influenced by both local- and landscape-level factors. Understanding how different biodiversity facets respond to biotic and abiotic factors across spatial scales remains challenging; yet this knowledge is essential for guiding management actions that support key ecological processes in agroecosystems. Here, we adopted a multi-taxa and multi-scale approach considering five groups: plants, bees, hoverflies, orthopterans, and birds. We assessed the effects of local management (annual mowing frequency, presence of uncut refuges) and landscape features (urban and agricultural cover, landscape heterogeneity) on taxonomic and functional diversity in managed grasslands. We found that multidiversity was positively associated with the presence of uncut refuges and with landscape heterogeneity, while it was negatively associated with urban and monoculture cover at the landscape level. The effect of mowing frequency was weak, potentially due to contrasting effects on different groups. Structural equation models showed that ecological effects varied across scales, groups, and biodiversity indicators: i) local scale management was particularly correlated with indicators of plants and hoverflies; ii) landscape scale factors had a stronger relationship with birds; iii) bees and orthopterans showed relationships at both local and landscape scales. Since different scales of agroecosystems management showed contrasting effects on different groups, we emphasize the importance of planning both local- and landscape-level management to embrace different facets of biodiversity.

1. Introduction

Starting from the late Prehistory, in many lowlands and mountains of Europe the opening of pristine forests for agropastoral land use often resulted in the formation of semi-natural grasslands (Hejcman et al., 2013; Mercuri et al., 2025; Stephens et al., 2019). In many areas, the long-term persistence of these environments is still controlled by human activities, being dependent on mowing or livestock grazing. Grasslands are among the most biodiversity-rich habitats in European agroecosystems, providing a broad spectrum of resources for a wide range of species (Dengler et al., 2014) meanwhile supporting key regulating ecosystem services, including pollination, pest control, and carbon storage (Bengtsson et al., 2019). Over the past century, European grasslands have significantly declined due to their conversion into more profitable crops, intentional afforestation, or the encroachment of trees and shrubs following progressive abandonment (Petermann and

---

* Corresponding author.
E-mail address: andrea.dalpasso@unimi.it (A. Dalpasso).

https://doi.org/10.1016/j.agee.2026.110257
Received 10 July 2025; Received in revised form 26 December 2025; Accepted 18 January 2026

Buzhdygan, 2021; Prangel et al., 2023). Additionally, the remaining managed grasslands have often undergone a strong intensification and mechanization of farming practices, leading to a dramatic reduction in their value in terms of biodiversity and ecosystem services (Bengtsson et al., 2019).

To halt the decline of grassland biodiversity and given the role of grassland soils as nature-based solutions for carbon stock, several agri-environmental practices have been implemented in Europe (Batáry et al., 2015; Phukubye et al., 2022). However, the effectiveness of these practices has often been limited and highly context-dependent, likely due to the influence of heterogeneous factors acting at both local and landscape scales (Pe'er et al., 2014; Scheper et al., 2013). For instance, local management practices such as the frequency and timing of mowing and the presence of uncut refuges are known to affect the survival of several invertebrates and grassland birds (Arbeiter et al., 2017; Humbert et al., 2012). Similarly, landscape factors such as landscape connectivity and surrounding land use have been shown to influence the richness of grassland birds (Assandri et al., 2019). The effects of these local- and landscape-level factors may vary across different taxonomic groups (Piano et al., 2017). For instance, previous studies found plant diversity to increase with mowing frequency (Bochniak et al., 2024), while the relationship is opposite for the diversity of orthopterans (Humbert et al., 2012). In contrast, birds and pollinators often show responses at the landscape scale, being positively associated with landscape heterogeneity and availability of natural elements (Dalpasso et al., 2025; Larkin and Stanley, 2021). Additionally, some factors may favor a given trait while disfavoring others. This may trigger changes in community composition without necessarily altering the number of species, potentially leaving important effects undetected when only taxonomic diversity is considered (Carmona et al., 2012; Purschke et al., 2013).

In agroecosystems, where functionality can play an important role also from a human perspective (e.g., pollination, pest control), it is crucial to understand the complex effects of management practices on both taxonomic and functional facets of biodiversity. These contrasting responses among different taxa and scales have often been investigated separately, and studies analyzing both taxonomic and functional diversity of different taxa remain rare (e.g., Simons et al., 2016; Torma et al., 2019). Yet, integrated analyses within a unified framework could provide a clearer understanding of how to manage grasslands in ways that sustain biodiversity across taxa and ecosystem functions. Moreover, studies are increasingly adopting multi-taxon metrics, such as multidiversity (Allan et al., 2014), to evaluate the overall response of agrobiodiversity to agricultural practices (Boetzl et al., 2021; Wang et al., 2019).

Here, we investigated the effects of both local (i.e., field-level) and landscape scale factors on the biodiversity of meadows (i.e., semi-natural grasslands as defined in Tälle et al., 2016), considering a broad ecological gradient within one of the most anthropized areas of Europe (i.e., agricultural landscapes of northern Italy). We integrated data on five different taxonomic groups: plants, bees, hoverflies, orthopterans, and birds, investigating how local management practices and the landscape surrounding meadows influence multidiversity. Additionally, we investigated taxon-specific effects on different facets of meadow biodiversity by considering both taxonomic and functional diversity metrics.

Specifically, we addressed the following questions:

- How do local management practices and landscape factors affect the biodiversity in meadows?

- Do these effects vary among taxonomic groups or depending on the facet of biodiversity considered (taxonomic vs. functional)?

We hypothesized that the effects of local management and landscape would not be uniform but taxon- and metric-specific, reflecting different ecological requirements. We expect that:

(1) Local management would have stronger effects on plants and orthopterans, due to their lack of (plants) or lower (orthopterans) mobility and high sensitivity to local disturbance and habitat structure (Batáry et al., 2012; Braschler et al., 2009; Humbert et al., 2012).

(2) Landscape factors would have stronger effects on bees, hoverflies, and birds, due to their higher mobility, which allows them to exploit the landscape at a broader spatial scale (Baker et al., 2012; Larkin and Stanley, 2021).

(3) Taxonomic and functional diversity do not necessarily exhibit congruent responses, as functional shifts may occur independently of changes in taxonomic richness (Purschke et al., 2013).

2. Materials and methods

2.1. Study area and field activities

The study area included 44 sites (i.e., meadows) located in northern Italy (Lombardy Region; Fig. 1). To include a broad variation in both local and landscape characteristics, we selected meadows spanning from the periphery of Milan city (the largest city of northern Italy), a strongly urbanized and industrialized area, to more rural hilly areas ~40 km from Milan (Fig. 1). A total of 13 areas (i.e., clusters) were selected, and these included 2–5 sites. Clusters were selected to maximize spatial representation within the study region and, within clusters, sites were selected to include variation in management practice and landscape characteristics. Within each cluster, the minimum distance between sites was on average 263 m (range 46 – 799 m), while the minimum distance between clusters (calculated based on the centroid of each cluster) was on average 6.6 km (range 3.6 – 13.1 km). Fieldwork activities were carried out from April to September 2024, to encompass most of the activity period of the five taxa considered in the study (plants, bees, hoverflies, orthopterans, and birds). Each taxon was sampled using specific field techniques that maximize the detection of species while minimizing the impact on local populations (i.e., less invasive methods were prioritized when possible).

Plant community data were collected using the quadrat sampling technique (Krebs, 1999), as it is a widely used and cost-efficient method that provides a fixed-area snapshot of plant community structure and ensures a consistent sampling effort across study sites (Kent, 2011; Krebs, 1999; Sutherland, 2006). Plant sampling activities took place between June and July 2024. For each site, we carried out a vegetation survey in five randomly placed 2 × 2 m quadrat plots, corresponding to a total of 20 m^2 of surveyed area per site (Fig. 1B). Plants were identified at the lowest taxonomic level possible following the taxonomic identification keys of Flora d'Italia (Pignatti et al., 2007) and Flora Helvetica (Lauber and Wagner, 1998; updated version on https://www.infoflora.ch).

Bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidae) were collected through targeted hand netting (Larsson and Franzén, 2008), as it is considered one of the best techniques to sample the entire bee community (Biella et al., 2025; Klaus et al., 2024; Lezzeri et al., 2024). Furthermore, unlike pan-traps, targeted hand netting avoids the indiscriminate capture and killing of non-target taxa, making it a more suitable and less harmful method for conducting surveys (Drinkwater et al., 2019; Popic et al., 2013), a vision recently shared by the EU Pollinator Monitoring Scheme (Potts et al., 2024). Each meadow was surveyed three times between June and July, with four 20 m long and 1 m wide transects conducted during each survey (Graham et al., 2024; Wider and Zemp, 2025; Fig. 1B). Transects were randomly placed within each site and survey. For each transect, all the individuals of the target taxa were collected using a butterfly net and conserved in 2 ml or 20 ml vials, depending on the specimen size. Honeybees (*Apis mellifera*) were counted but not captured due to their easy identification and high number of individuals found. Finally, all collected specimens were identified at the lowest taxonomic level possible under a stereomicroscope following taxonomic identification keys (Amiet et al., 2014; Bertollo and Sommaggio, 2012; Cappellari et al., 2018; Michez et al., 2019, 2004; Van Veen, 2004).

Orthopterans were captured through sweep netting along transects,

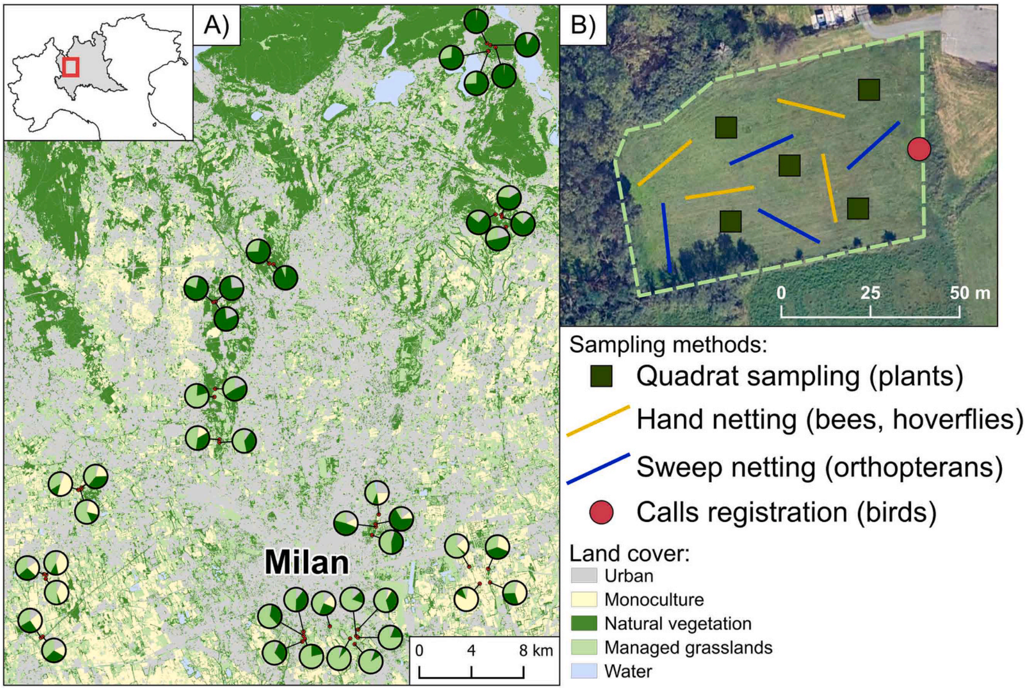

Fig. 1. Study sites and sampling methods used. (A) Location of the study sites in northern Italy. The position of the study area is shown with a red rectangle in the top-left inset, also showing the Lombardy region in grey. The colors in the main map represent urban areas (grey), monocultures (yellow), natural vegetation (dark green), managed grasslands (light green), and water (azure). The exact location of study sites is marked by red circles, while pie charts show the percentages of land cover in the 200 m surrounding each site. (B) Example of the sampling scheme used. Green squares represent vegetation plots; yellow and blue lines represent transects for pollinators and orthoptera respectively; the red circle represents the microphone placed for bird calls registration.

one of the most used methods for sampling orthopterans (Nodari et al., 2025; Stoch and Genovesi, 2016). This technique consists of sweeping the surrounding vegetation with a net by repeatedly doing a left-to-right arc in front of the observer. Each meadow was surveyed five times from June to September and, within each survey, we performed four 20 m transects to ensure comprehensive coverage of the entire area (Fig. 1B). Transects were randomly placed within each site and survey and were independent from the ones of bees and hoverflies. We performed 20 sweeps in each transect, maintaining a rate of ~1 sweep per meter (Nodari et al., 2025). All captured individuals were identified at the lowest taxonomic level possible in the field and then released. In a few cases, when field identification was not possible, individuals were collected in 2 ml vials and then identified under a stereomicroscope following taxonomic identification keys (Iorio et al., 2019; Massa et al., 2012).

Bird data were collected through passive acoustic monitoring, a cost-effective, non-invasive technique widely used to estimate songbird occurrences and whose application in ecological studies has rapidly increased in recent years (Pillay et al., 2019; Sugai et al., 2019). Bird census activities were performed between April and June (a period corresponding to the peak of the breeding season of most species in the area) and concentrated in the first hours following the sunrise, when birds are more vocally active for territorial purposes (Gagliardi and Tosi, 2012). We visited each meadow four times and, in each survey, we placed a directional microphone (Zoom H1n) oriented towards the meadow to record environment sounds for 15 min (Fig. 1B). Finally, each recording was reviewed by a single user to identify birds at the species level, with the combined assistance of Merlin (https://merlin.allaboutbirds.org/) and BirdNET (https://birdnet.cornell.edu/), two widely used software for songbird identification (Pankiv and Kloetzer, 2024).

2.2. *Biodiversity metrics*

To assess the impact of local management and landscape factors on different facets of biodiversity, for each taxon and site, we calculated four metrics: taxonomic richness (number of species), functional identity (i.e., community position in the functional space; Mouillot et al., 2013), functional diversity, and functional redundancy. Data elaboration and statistical analyses were performed in R environment (R Core Team, 2023).

The number of species was calculated by summing up the different taxonomic entities found at each site. Individuals/specimens identified at the genus level were treated as additional species when they clearly represented a different entity from those already recorded at the site. Rare species – defined as those occurring in $< 30\ \%$ of the spatial or temporal replicates within a given site (i.e., a meadow) – were excluded from the analyses (Appendix S1) as, in the specific context of our study design and goals, they can bias results due to their limited importance for trophic relationships and ecosystem functioning (Poos and Jackson, 2012).

For the three functional metrics, we started by retrieving functional traits data at species-level resolution from multiple databases, publications, and manuals (Table S1). From the full set of available traits, we selected those that met three key criteria: i) data availability, ii) broad applicability among species, and iii) consistency with our study design (e.g., given the focus on a single habitat, all traits describing habitat preferences were not considered). In our analyses, we included 11 traits for plants: dispersion syndrome, exoticism, flowering season, growth form, height, leaf carbon content, leaf nitrogen content, leaf area, nitrogen fixation capacity, pollination syndrome, seed dry mass; four traits for bees: body size, diet, nesting, sociality; four traits for hoverflies: flight period (seasonal phenology), flower visits, larva feeding strategy, mean size; five traits for orthopterans: dispersion strategy, adult phenology, diet, mobility, mean size; four traits for birds: primary lifestyle, mean mass, trophic level (carnivore, herbivore, or omnivore), trophic niche (diet type). The trait dataset assembled for this work is available in Appendix S2.

All functional metrics were calculated separately for each taxonomic group, using group-specific trait-based distance matrices and presence–absence community matrices, excluding rare species as done for taxonomic richness. Pairwise trait dissimilarities between species were computed using Gower's distance, which accommodates both continuous and categorical traits, using the "gowdis()" function from R package *FD* (Laliberté et al., 2014). Categorical traits were fuzzy coded, and when a trait was represented by multiple categories, category weights were adjusted so that each trait contributed equally to the overall distance, irrespective of the number of categories. Continuous traits were used as raw values and assigned equal weight (1). Functional diversity was quantified using Rao's quadratic entropy, which measures

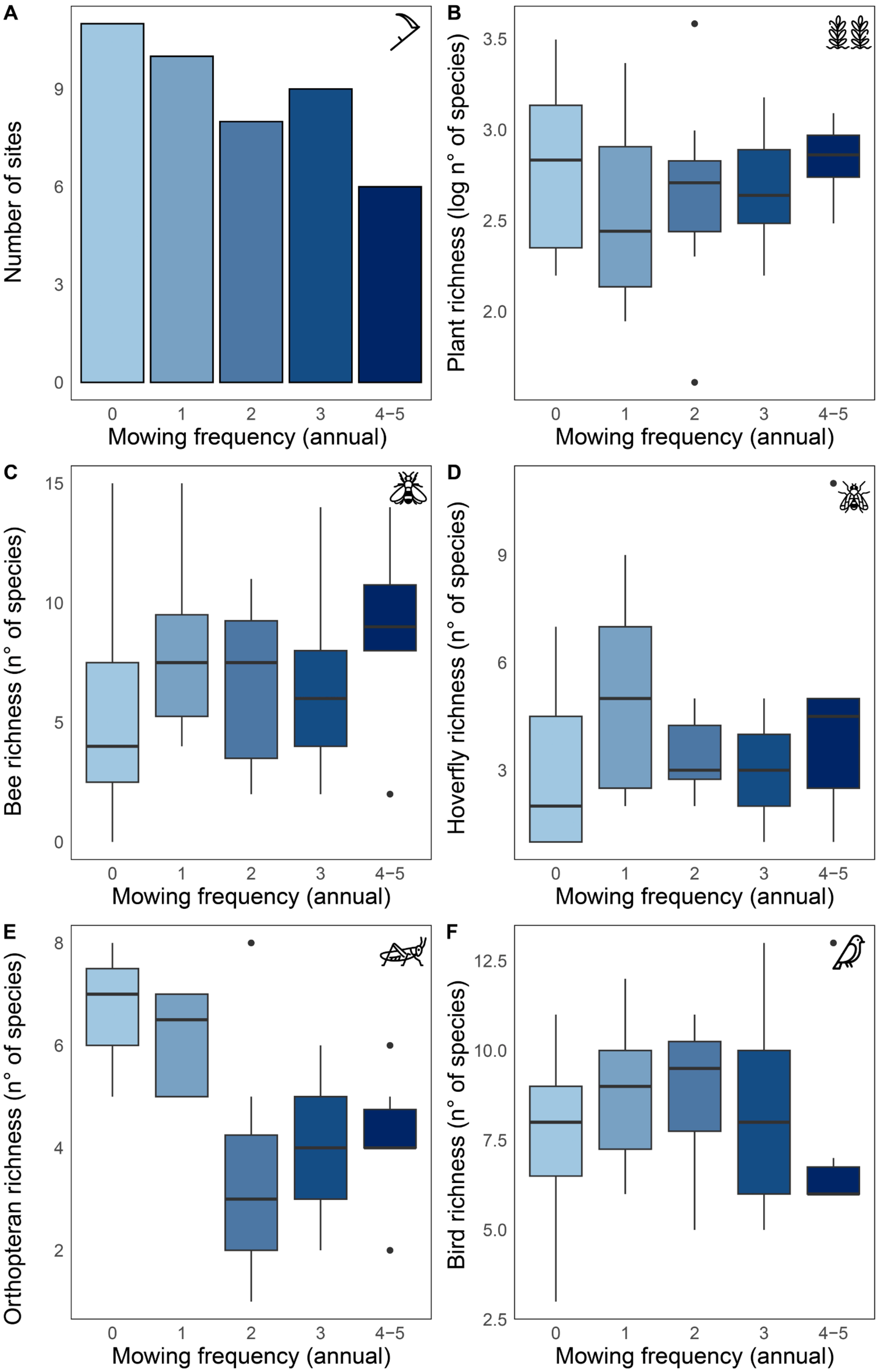

Fig. 2. Mowing frequency across the 44 study sites (A) and boxplots of the number of species across mowing frequency categories, for the five groups considered (B–F). Panels B–F show the number of species of (B) plants (log-transformed), (C) bees, (D) hoverflies, (E) orthopterans, (F) birds (for boxplots, lines: median, box: interquartile range, whiskers: 1.5 times interquartile range, points: data above or below 1.5 interquartile range).

the average trait dissimilarity between all species pairs in a community, integrating both species composition and trait differences (Rao, 1982), following the approach of de Bello et al., (2010). Since our data were presence–absence, all species were treated equally, capturing trait dissimilarity among co-occurring taxa regardless of abundance. Functional redundancy refers to the extent to which species within a community share similar trait combinations, leading to overlap in functional roles (Rosenfeld, 2002). It was estimated using the "rao.diversity()" function from the R package *SYNCSA* (Debastiani and Pillar, 2012). To assess functional identity, we conducted Principal Coordinates Analysis (PCoA) on each group-specific distance matrix and retained the first two axes to construct a bidimensional functional space (Mouillot et al., 2013). Species were projected into this space and traits were fitted onto the PCoA ordination using the "envfit()" function from the R package *vegan* (Oksanen et al., 2022) to identify which traits were most discriminant in the functional space. Traits with high R^2 values and significant *p*-values were considered important contributors to trait dissimilarity within the functional space. Functional identity for each site was then calculated as the mean position of all species present at that site along the first PCoA axis, reflecting the dominant trait composition of the community (Mouillot et al., 2013). Interpretation of functional identity responses to predictors requires referencing the functional space: a positive relationship with a given axis suggests a shift toward traits located at the positive end of that axis, while a negative relationship indicates selection for traits on the opposite end.

Finally, to evaluate effects on the overall community sampled, we calculated a "multidiversity index", which synthesizes the overall taxonomic richness, standardized across the groups considered. In so doing, we rescaled species richness for each of the five groups between zero and one; then, rescaled values were averaged for each site (Allan et al., 2014).

2.3. *Local and landscape predictors*

As candidate predictors of taxonomic and functional diversity of all groups, we considered the following variables: i) mowing frequency, ii) presence of uncut refuges, iii) distance from Milan metropolis and elevation (hereafter "spatial context"), iv) extent of urban and monoculture land cover, and v) landscape heterogeneity. The first two predictors captured the influence of local scale management, while the latter three represented landscape scale effects. Annual mowing frequency and the presence of uncut refuges were assessed through direct observation in the field. Overall, the mowing frequency observed at the monitored sites ranged from 0 to 5 cuts per year. Across the 44 sites, only six sites had more than three mowing events (Fig. 2).

The "spatial context" variable was considered as a control factor describing processes acting at a regional scale. We accounted for the effect of two factors that are co-varying in the study region: distance from Milan (the nearest metropolis) and elevation. Distance from Milan metropolis ranged from 4.6 to 42.9 km (quantiles: Q1 = 6.7 km; Q2 = 16.8 km; Q3 = 22.3 km). Elevation ranged from 102 to 676 m asl (Q1 = 110 m asl; Q2 = 138 m asl; Q3 = 250 m asl). Hence, elevation shows a relatively low variation among plots as all study sites are located within the lowland or the hill belt. To account for this covariation and calculate the "spatial context" variable, we performed a Principal Component Analysis (PCA) obtained between the site's distance from the city center of Milan and its elevation. The first axis of the PCA explained 94.7 % of the variance and was positively related to both the distance from Milan and elevation (Figure S1). Although the relationship between the spatial context variable and our response variables are shown in the results, we will not discuss them further in the results section, as we cannot disentangle the effects of elevation and distance from the metropolis.

To estimate urban and monoculture cover around each site, we used the EUSALP land use/land cover map (pixel resolution: 5 m; Marsoner et al., 2023). For each site, we defined a 200 m radius and extracted the proportions of all land use categories within that area. We chose a 200 m radius as we can reasonably assume that most of the species considered in our study areas are affected by land use changes at this scale (Batáry et al., 2007; Brambilla et al., 2024; Dauber et al., 2003; Toikkanen et al., 2022). Categories associated with settlements, roads, and monocultures were grouped to calculate "urban and monoculture cover". Then, to take into account landscape heterogeneity, we calculated the Shannon Diversity Index based on the proportional distribution of the different land use categories (Estrada-Carmona et al., 2022). In so doing, based on ecological similarity, we aggregated the original 36 categories present in the landscapes around study sites, obtaining a total of 9 categories, including: urban, managed grasslands, tall crops, short crops, broadleaves, conifers, woody features, scrub and shrubland, water bodies (Table S2).

2.4. *Data analysis*

To evaluate effects on multidiversity, we performed a linear model with the multidiversity index as dependent variable and using local (mowing frequency and presence of uncut refuges) and landscape (spatial context, urban and monoculture cover, landscape heterogeneity) variables as predictors. As preliminary plots did not show clear evidence for quadratic effects (Figure S2), we included only linear terms.

To assess the relationships among different components of managed meadows, we used structural equation models (SEM), which represent a more robust approach than multiple linear analyses, accounting for direct, indirect, and total effects of predictor variables (Grace, 2006). SEM models were implemented using R package *lavaan*, version 0.6–19 (Rosseel, 2012). We started from an a priori causal structure, a comprehensive model including all possible links from the five local and landscape variables to the five taxa and also two covariations (plants–bees, and plants–hoverflies; Figure S3). Then, we progressively removed strongly non-significant links ($p > 0.5$) to improve models' fit (Rahman et al., 2021). The removal of each link was accepted if model's Akaike information criterion (AIC) was improved (Jiao et al., 2021). The selection of the final model among competing alternatives was guided by goodness-of-fit statistics and the AIC. To assess model fit, we checked commonly recommended indices (Schermelleh-Engel et al., 2003): the root mean square error of approximation (RMSEA, with values < 0.05 indicating good fit), the Tucker–Lewis index (TLI, with values > 0.95 indicating good fit), the comparative fit index (CFI, with values > 0.95 indicating good fit) and the chi-squared test (CHI, with $p > 0.05$ indicating good fit). We fitted four different SEM, differing in the type of response variable considered for our groups: i) taxonomic richness, ii) functional identity, iii) functional diversity, and iv) functional redundancy.

Before running the analyses, community data for all groups were screened for distributional properties, checking normality with Shapiro-Wilk test (Shapiro and Wilk, 1965); consequently, plant species richness was log-transformed to reduce skewness. Collinearity among predictors was checked and our dataset did not show any strong collinearity (|Pearson's correlation coefficient| always < 0.7; Figure S4).

3. Results

Overall, we identified: 282 species of plants (mean ± SD = 28.5 ± 10.3 species per site), 97 species of bees (6.9 ± 3.9 per site), 33 species of hoverflies (3.8 ± 2.3 per site), 34 species of orthopterans (8.4 ± 2.7 per site), and 54 species of birds (14.2 ± 3.4 per site) (Appendix S1).

3.1. *Effects on multidiversity*

The linear model assessing the relationships between local management factors and the multidiversity index was statistically significant ($F_{5,38} = 5.502$, $p < 0.001$; adjusted $R^2 = 0.344$). Diagnostic plots suggested that assumptions of linear regressions were satisfied (Figure S5).

The presence of uncut refuges showed a positive and significant relationship with multidiversity (β = 0.154, $p = 0.004$; Table S3; Fig. 3), while this was not the case for the number of mowing events ($p = 0.966$). At the landscape-level, multidiversity was negatively related to urban and monoculture cover (β = −0.256, $p = 0.034$) and positively related to landscape heterogeneity (β = 0.173, $p = 0.024$). Additionally, the "spatial context" variable showed a positive relationship (β = 0.048, $p = 0.003$), meaning that multidiversity was higher far from Milan.

3.2. *Group-level effects on taxonomic and functional diversity*

Functional spaces showed that the first axis of the PCoA was strongly related to a different number of traits for the different groups (Table S6; Fig. 4). In plants, PCoA axis 1 described a functional gradient with negative scores associated with non-nitrogen-fixing, wind-pollinated species and positive scores associated with nitrogen-fixing, insect-pollinated species. Among bees, axis 1 contrasted medium-sized, oligolectic, solitary species with small-sized, parasitic species that neither nest nor collect pollen. For hoverflies, axis 1 contrasted species with an early flight season from flower specialists. For orthoptera, axis 1 differentiated larger, phytophagous species, with higher flight capacity, from smaller omnivores with higher jump/walk capacity and ground dispersion. Finally, in birds, axis 1 opposed small species, with an insessorial (i.e., adapted for perching) lifestyle, an invertivore trophic niche, and a carnivore trophic level, to larger species, with a terrestrial lifestyle, omnivore trophic niche, and herbivore trophic level.

All SEM showed good fit indices, with RMSEA < 0.05, TLI > 0.95, CFI > 0.95, and *p*-values of CHI > 0.05 for all models (Table S4). The four biodiversity metrics showed different relationships with local and landscape factors, with 10 significant relationships for the taxonomic richness model, 12 for the functional identity model, and 5 for both the functional diversity and functional redundancy models (Table S5; Fig. 5). In the sections below, for each group, we describe only significant effects ($p < 0.05$).

3.2.1. *Plants*

Our modelling results showed that only local scale management factors were significantly related to plant diversity, while none of the landscape factors had a significant effect (Fig. 5; Table 1). Mowing frequency had no detectable effect on plant taxonomic richness and on functional diversity (Fig. 5A, C), while it was significantly and positively related to functional identity along the first axis of the plant functional space (Fig. 5B). High mowing frequency was associated with positive

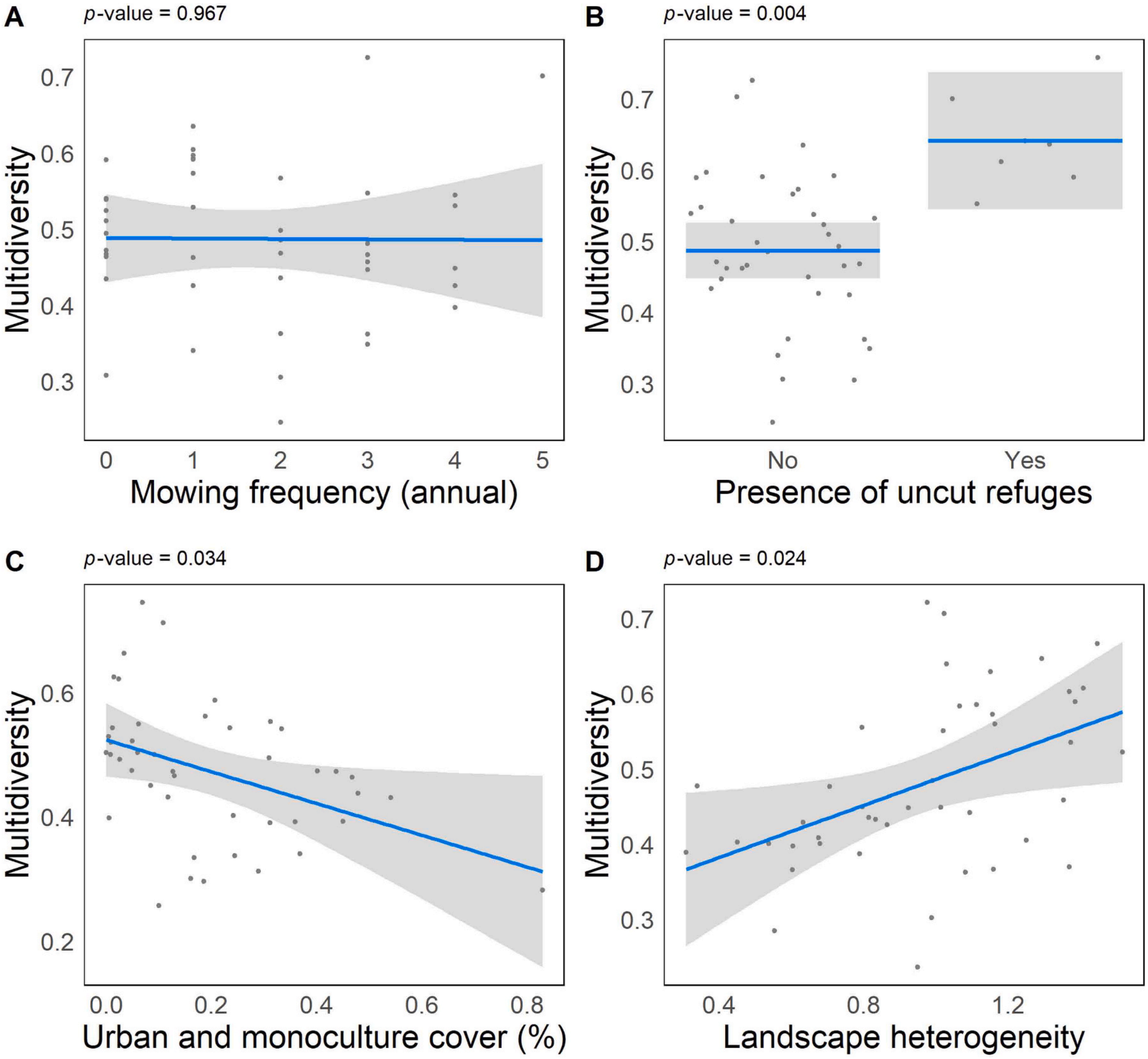

Fig. 3. Effects of local management and landscape features on multidiversity of managed meadows. Marginal response plots of: (A) annual mowing frequency, (B) presence of uncut refuges, (C) urban and monoculture cover in the surrounding landscape, and (D) landscape heterogeneity. Blue lines and grey shades represent average prediction and 95 % confidence intervals. The grey points represent the residuals, and in B they are randomly scattered on the horizontal axis to avoid excessive overlap.

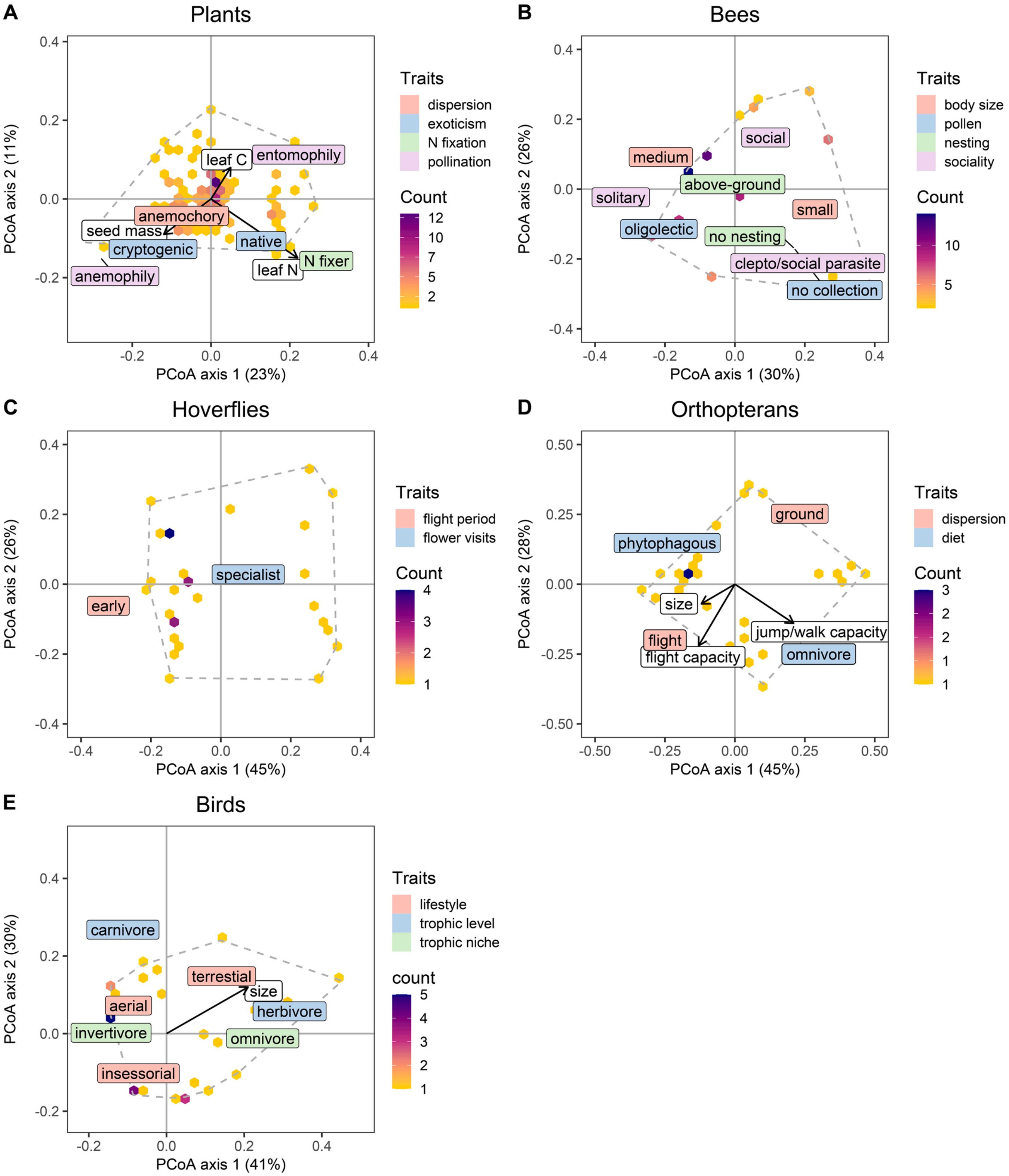

Fig. 4. Functional spaces for the five groups considered (plants, bees, hoverflies, orthopterans, birds). Each panel represents the first two axes of the PCoA, with the percentage of variation represented by each axis shown within parentheses. Hexagons represent the position of species within the functional space and are colored based on the number of overlapping species (count). The colored labels represent subcategories of categorical traits, and continuous traits are indicated with an arrow and a white label. To highlight the main ecological gradient represented by the first PCoA axis, we only displayed traits with a significant fit ($p < 0.05$) to the ordination and oriented primarily along that axis (i.e., vectors with direction cosines $> |0.5|$ on Axis 1). See Table S6 for detailed results of the fitting analysis (direction cosines, R^2, and p for each trait category).

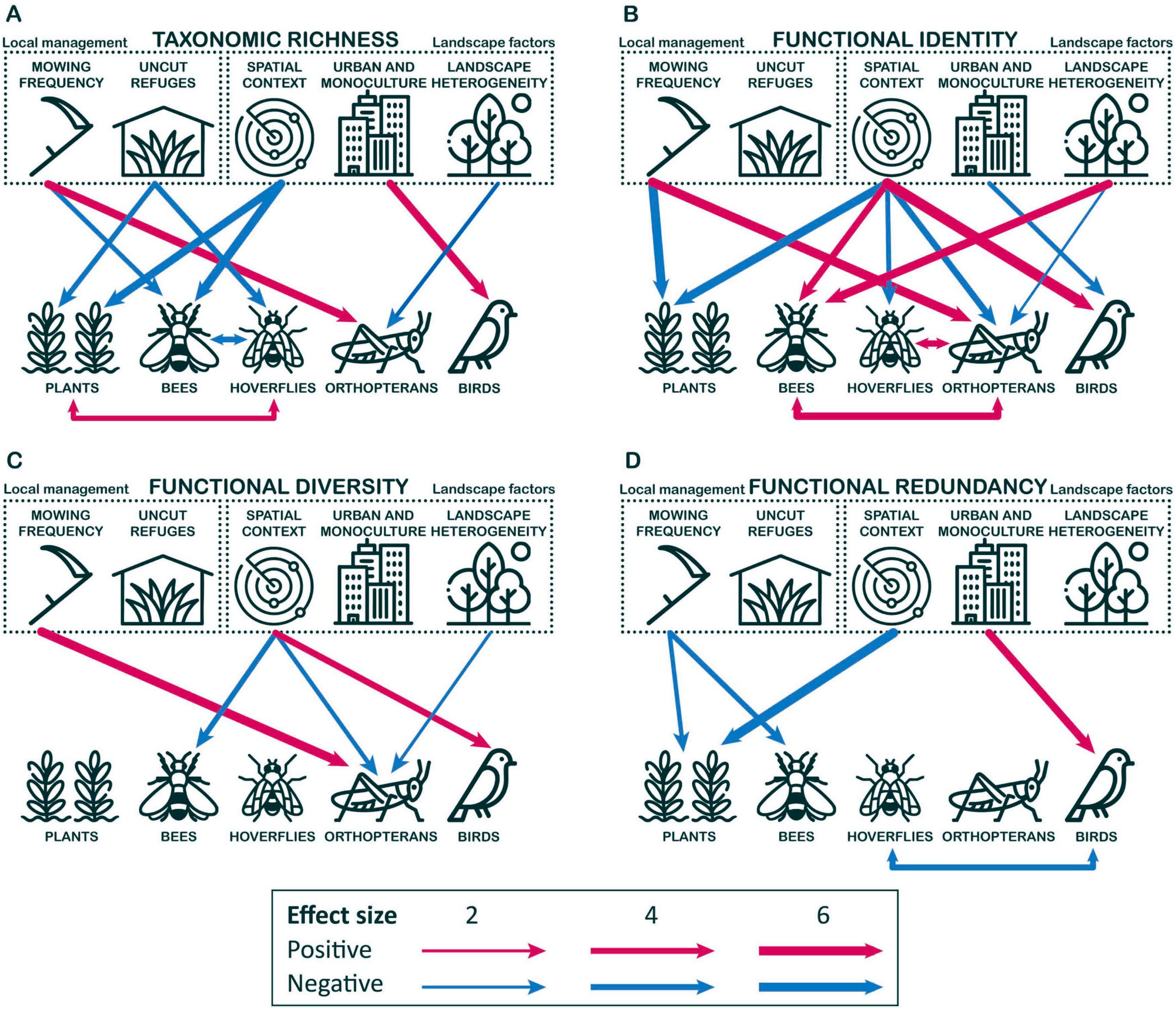

Fig. 5. Results of structural equation models showing relationships between local management and landscape features with different diversity metrics for five groups. The four panels show (A) taxonomic richness, (B) functional identity, (C) functional diversity, (D) functional redundancy. Arrows show only significant relationships, with blue arrows indicating positive relationships and red arrows negative relationships (arrow widths are proportional to standardized partial effect sizes, shown in Table 1). All the parameter estimates, including non-significant relationships, are in Table S5.

scores along the first axis of the functional space, reflecting communities dominated by nitrogen-fixing and insect-pollinated (entomophilous) species (Fig. 4A). This, in our dataset, largely corresponds to Fabaceae (e.g., species from the genera: *Trifolium*, *Lotus*, *Medicago*, *Vicia*; Appendix S2). Moreover, functional redundancy was positively related to mowing frequency, meaning that single traits are covered by more species in meadows with more mowing events (Fig. 5D). The presence of uncut refuges showed a positive relationship with taxonomic richness but had no detectable effects on functionality.

3.2.2. *Bees*

Both local scale management and landscape scale factors affected bee diversity (Fig. 5; Table 1). Both bee taxonomic richness and functional redundancy were higher at higher mowing frequencies (Fig. 5A, D), but no significant effects were found on functional identity or functional diversity (Fig. 5B, C). At the landscape scale, landscape heterogeneity was associated with a shift in functional identity towards community dominated by medium-sized, oligolectic, solitary, and above-ground hole-nesting species (Fig. 4B; Fig. 5B). This, in our dataset, largely corresponds to Megachilidae (Appendix S2).

3.2.3. *Hoverflies*

The presence of uncut refuges was positively related to taxonomic richness of hoverflies (Fig. 5A), while none of the landscape scale management factors or mowing frequency had a detectable effect (Fig. 5; Table 1).

3.2.4. *Orthopterans*

Both local and landscape scale management factors affected orthopteran diversity (Fig. 5; Table 1). Mowing frequency showed a strong negative effect on orthopteran taxonomic richness, while being associated with a shift in functional identity towards species with higher flight capacity, larger, and phytophagous (Fig. 4D; Fig. 5B). On the other hand, no significant effect of uncut refuges was found. At the landscape scale, landscape heterogeneity showed a positive effect on taxonomic richness and functional diversity (Fig. 5A, C). Landscape heterogeneity

Table 1

Proposed interpretations of significant effects found in the four structural equation models analyzing relationships between local management and landscape features and five biodiversity groups. The column "Magnitude" shows standardized partial effect sizes (and standard errors), with colors representing positive (blue) and negative (red) effects. For each biodiversity metric, effects are ranked by magnitude. All parameter estimates are available in Table S5.

Effect	Magnitude	Proposed interpretation
Taxonomic richness		
Mowing frequency → Orthopterans	-0.533 (0.113)	Direct mortality, habitat loss, reduced vegetation complexity.
Urban and monoculture cover → Birds	-0.516 (0.156)	Habitat fragmentation, noise, reduced availability of nesting and foraging sites.
Uncut refuges → Hoverflies	0.383 (0.134)	Prolonged nectar and pollen availability.
Mowing frequency → Bees	0.318 (0.130)	Increased floral turnover, reduced competition.
Landscape heterogeneity → Orthopterans	0.260 (0.124)	Greater variety of habitats, niches, and preys.
Uncut refuges → Plants	0.350 (0.105)	Reduced disturbance, differential turnover.
Functional identity		
Mowing frequency → Orthopterans	-0.609 (0.063)	Katydids are disfavored due to their lower fertility and reduced mobility.
Mowing frequency → Plants	0.596 (0.102)	Fabaceae are favored due to lower competition with Poaceae.
Landscape heterogeneity → Bees	-0.554 (0.138)	Megachilidae are favored with more floral resources and nesting habitats.
Urban and monoculture cover → Birds	-0.314 (0.120)	Larger, omnivorous birds are favored as they are often synanthropic.
Landscape heterogeneity → Orthopterans	0.170 (0.084)	Katydids are favored due to increased availability of diverse prey resources.
Functional diversity		
Mowing frequency → Orthopterans	-0.586 (0.086)	Habitat disturbance and reduced vegetation complexity.
Landscape heterogeneity → Orthopterans	0.216 (0.108)	Greater variety of habitats, niches, and preys.
Functional redundancy		
Urban and monoculture cover → Birds	-0.515 (0.104)	Reduced availability of nesting and foraging sites, increased competition.
Mowing frequency → Bees	0.362 (0.150)	Reduced competition leads to coexistence of functionally similar species.
Mowing frequency → Plants	0.294 (0.129)	Reduced competition leads to coexistence of functionally similar species.

was also associated with changes in functional identity underlined by a higher representation of species with better jump/walk capacity, with ground dispersion, and omnivore (Fig. 4D; Fig. 5B). This, in our dataset, corresponds to brachypterous bush crickets (Appendix S2).

3.2.5. *Birds*

Birds showed relationships with landscape-level factors only (Fig. 5; Table 1). At the taxonomic level, urban and monoculture were negatively related to species richness (Fig. 5A), while at the functional level the increase in urban and monoculture land uses was associated with an overrepresentation of larger herbivores and omnivores, with a terrestrial lifestyle (Fig. 4E; Fig. 5B), and to a reduced functional redundancy (Fig. 4E; Fig. 5D).

4. Discussion

Our study shows that both local management and landscape features could affect multidiversity of managed meadows, although their effects vary across trophic groups and biodiversity metrics.

4.1. *Effects of local management and landscape factors on multidiversity*

Multidiversity was higher in the presence of uncut refuges and in landscapes with a lower agricultural and monoculture cover but higher landscape heterogeneity. Leaving some portions of the meadow uncut can increase the number of individuals rescued from mowing events, also providing more stable habitats from where individuals can recolonize mown portions of the meadow (Buri et al., 2013; Humbert et al., 2012). Urban environments and monocultures are usually associated with low biodiversity due to habitat homogenization and eco-physiological stress induced by the characteristics of these environments, such as decrease in resource availability, use of pesticides, or increase in extreme temperature events (Wenzel et al., 2023). Finally, the positive relationship between landscape heterogeneity and multidiversity is expected, since more diverse landscape can host more species due to the presence of more ecological niches (Assandri et al., 2016; Muñoz-Sáez et al., 2021).

Unexpectedly, we found no relationship between the number of mowing events and multidiversity. On the one hand, the mowing intensity was generally low, with most sites being cut two times or less. On the other hand, the flat relationship between mowing intensity and multidiversity may be the outcome of contrasting effects on different groups. While meta-analysis on urban grasslands suggested a general negative effect of mowing on arthropods (Proske et al., 2022), mowing can be beneficial for some groups (Noordijk et al., 2009). In this study, when analyzing group-level effects, we found a positive effect of mowing intensity on taxonomic diversity of bees, and a negative effect on orthopterans. This result stresses the importance of interpreting effects on multidiversity in light of group-specific relationships, that may be masked when a single analysis is performed (Werling et al., 2014).

4.2. *Group-level effects on taxonomic and functional diversity*

We initially expected plant taxonomic and functional diversity to increase with mowing, particularly given that most of sampled sites were cut two times or less per year, and only six sites had more than three mowing events. However, previous studies have shown that different mowing regimes can yield similar effects on plant species richness, which is largely driven by local, habitat-specific factors (Tälle et al., 2018). This may account for the lack of relationships between mowing and either plant taxonomic richness or functional diversity in this study. Our results are consistent with previous findings indicating that mowing can promote a process of functional convergence in many traits, thus increasing functional redundancy (Guerra et al., 2022; Mudrák et al., 2016). This is because low-intensity mowing can reduce interspecific competition and encourage the coexistence of functionally similar species (Halassy et al., 2019). Finally, while previous studies have emphasized the importance of uncut refuges for arthropod diversity without detrimental effects on plant communities (Révész et al., 2025; Rossier et al., 2023), our analyses suggest that such refuges may also actively enhance plant diversity. This means that although low-intensity mowing can benefit plant stability (i.e., higher redundancy of certain traits, likely nitrogen fixing capacity and entomophily; Hassan et al., 2023), it remains important to maintain uncut portions of grasslands to promote local plant diversity in the studied system.

Regarding pollinators (bees and hoverflies), our results indicate that mowing supports a greater number of bee species, which perform similar ecological roles but without introducing new functional traits into the community (i.e., higher functional redundancy and no effect on functional diversity). As shown in previous studies, mowing can benefit flower-visiting insects (Noordijk et al., 2009). In our study system, we showed that low-frequency mowing is related to higher redundancy of entomophilous species; this means that plants with more attractive flowers for pollinators (i.e., Fabaceae family) are favored. In contrast, in urban environments, where resources can be lower and mowing frequencies much higher, it has been shown that reducing mowing frequency promotes greater bee diversity (Biella et al., 2025). Results also showed that landscape heterogeneity favors medium-sized, oligolectic, solitary species. Our findings reflect other research that found more large-bodied and social bees and less oligolectic species in highly homogeneous environments (such as urban areas with highly fragmented green spaces; Ferrari and Polidori, 2022). These differences are likely driven by the availability of floral resources and nesting sites, which are more diverse in heterogeneous agricultural landscape (Cavigliasso et al., 2022). The observed positive effect of uncut refuges on taxonomic diversity of hoverflies aligns with the findings of Meyer et al. (2017), who suggest that experimentally prolonged resource availability – such as nectar and pollen – may explain the increased abundance and richness of hoverflies in uncut areas.

We observed a negative impact of mowing frequency on orthopterans, aligning with extensive literature knowledge (Braschler et al., 2009; Fumy et al., 2021). Brachypterous bush crickets appeared to be disadvantaged at higher mowing frequencies, and this is likely due to their lower fertility (measured as the number of laid eggs) and reduced mobility, as indicated by Ancillotto and Labadessa (2024). The experiment conducted by Braschler et al. (2009) highlighted the reluctance of bush crickets to venture into mown areas, confirming the low suitability of intensively managed habitats. We expected a positive effect of uncut refuges on orthopteran taxonomic and functional diversity (Buri et al., 2013; Kaláb et al., 2020), but no such effect was observed. However, refuges typically influence local orthopteran populations more in terms of biomass and density (Humbert et al., 2012), metrics that were not assessed in our study. Our results also corroborate the idea that landscape heterogeneity fosters taxonomic richness of orthopterans (Löffler and Fartmann, 2017). The observed enhancement of orthopteran functional diversity and the concurrent shift in functional identity towards brachypterous bush crickets at higher landscape heterogeneity are likely attributable to the increased availability of diverse prey resources, supporting their omnivorous diet regime (Biella et al., 2025).

Birds showed responses mainly at the landscape level, with a negative effect of urban and monoculture cover on taxonomic richness, which reflects the generally negative impact of anthropic landscapes on bird diversity (Silva et al., 2015). We would have expected a positive effect of landscape heterogeneity, which is widely known to positively influence bird diversity (Assandri et al., 2016; Dalpasso et al., 2025). This lack of relationship could be related to the fact that many grassland birds (like the skylark) need non-fragmented large open spaces (Cramp, 1998), thus indicating that the positive effect of landscape heterogeneity may be species- and spatial scale-specific (Dvoráková et al., 2023).

4.3. Study limitations

The main limitation of the study is the relatively low number of study sites, which hampers the evaluation of more complex relationships. For instance, non-linear responses (e.g., quadratic relationships) between local or landscape factors and biodiversity metrics may exist. However, including polynomial terms would likely have led to overfitting of structural equation models, given the high number of potential links compared to the sample size (Westland, 2019). Nevertheless, the selected meadows spanned a broad environmental gradient, from urban to rural areas, offering the opportunity to capture a wide spectrum of management and landscape conditions.

Birds were mostly surveyed from the meadow edge. Even if the directional microphone was oriented towards the center of the sampled meadow, it is possible that some individuals outside the meadows also entered the recordings and hence the dataset. This is unlikely to significantly affect any outcomes, and the overall importance of landscape features for birds is much more likely related to their ecology than to sampling biases, considering the relevance of landscape composition and configuration for avian taxa and communities (Anderle et al., 2022; Granata et al., 2025). We also highlight that birds are highly mobile, and individuals perching at the meadow edge can then enter into the meadow, for instance for feeding.

To our knowledge, this study represents one of the first attempts to integrate multiple biodiversity metrics (taxonomic and functional) across several taxonomic groups in semi-natural grasslands. Still, additional groups can play key roles in grassland ecosystems. For instance, soil biota and mesopredators (e.g., spiders) can be valuable additions to future multi-taxa studies on meadow's biodiversity (Oyarzabal and Guimarães, 2021; Wu et al., 2023).

5. Conclusions

Our study shows that: i) local scale (i.e., field) management mainly affected plants and hoverflies; ii) landscape scale factors had stronger effects on birds; and iii) orthopterans and bees showed responses at both scales (Fig. 4); these results partially supported hypotheses 1 (local scale effects are stronger for plants and orthopterans) and 2 (landscape scale effects are stronger for bees, hoverflies, and birds). Biodiversity responses were also metric-specific, supporting hypothesis 3 (taxonomic and functional diversity are not always congruent).

Given the complex group-specific impacts of local- and landscape scale factors, adopting a multi-taxa and multi-scale perspective offers a comprehensive framework to better understand how to plan agricultural land management under a biodiversity conservation perspective. For instance, a simple and effective management measure to increase diversity can be the maintenance of uncut refuges, which were likely to support higher taxonomic diversity of plants and hoverflies, and higher functional diversity of birds, without any detrimental effect on other groups. Moreover, since landscape heterogeneity likely supports key groups such as pollinators and orthopterans, we emphasize that it should be a central component when planning agricultural landscape management.

Data availability

The dataset and script used to run the analyses are available at Figshare: https://doi.org/10.6084/m9.figshare.29382995.v1

CRediT authorship contribution statement

Matteo Conti: Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andrea Dalpasso:** Writing – original draft, Methodology, Investigation. **Alberto Mattia Nodari:** Writing – review & editing, Visualization, Resources, Investigation, Data curation. **Isabel Cantera:** Writing – original draft, Visualization, Methodology, Formal analysis. **Benedetta Barzaghi:** Writing – review & editing, Resources. **Mattia Brambilla:** Writing – review & editing, Resources. **Andrea Ferrari:** Writing – review & editing, Resources. **Gentile Francesco Ficetola:** Writing – review & editing. **Simone Giachello:** Writing – review & editing. **Elia Lo Parrino:** Writing – review & editing, Resources. **Valeria Messina:** Writing – review & editing, Resources. **Carlo Polidori:** Writing – review & editing. **Michele Pozzi:** Writing – review & editing, Investigation. **Sofia Redaelli:** Resources, Investigation. **Andrea Zerboni:** Writing – review & editing, Resources. **Gianalberto Losapio:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Mattia Falaschi:** Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Funding

This research was funded by the University of Milan under the "My First SEED Grant" fund, DM 737/2021 MUR.

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

We thank all the landowners and protected areas that provided permission to perform field sampling (Parco del Monte Barro, Parco di Montevecchia e della Valle del Curone, Parco delle Groane, Parco Agricolo Sud Milano). We are grateful to L. Trainelli and P. Rantiprati for their help during the fieldwork.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110257.

Data availability

The dataset and script used to run the analyses are available at Figshare: https://doi.org/10.6084/m9.figshare.29382995.v1

References

Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tscharntke, T., Blüthgen, N., Bellach, M., Birkhofer, K., Boch, S., Böhm, S., Börschig, C., Chatzinotas, A., Christ, S., Daniel, R., Diekötter, T., Fischer, C., Friedl, T., Glaser, K., Hallmann, C., Hodac, L., Hölzel, N., Jung, K., Klein, A.M., Klaus, V.H., Kleinebecker, T., Krauss, J., Lange, M., Morris, E.K., Müller, J., Nacke, H., Pašalić, E., Rillig, M.C., Rothenwöhrer, C., Schall, P., Scherber, C., Schulze, W., Socher, S.A., Steckel, J., Steffan-Dewenter, I., Türke, M., Weiner, C.N., Werner, M., Westphal, C., Wolters, V., Wubet, T., Gockel, S., Gorke, M., Hemp, A., Renner, S.C., Schöning, I., Pfeiffer, S., König-Ries, B., Buscot, F., Linsenmair, K.E., Schulze, E.D., Weisser, W.W., Fischer, M., 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proc. Natl. Acad. Sci. 111, 308–313. https://doi.org/10.1073/pnas.1312213111.

Amiet, F., Herrmann, M., Mueller, A., Neumeyer, R., 2014. Apidae 4: Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis, Fauna helvetica 9. Centre Suisse de Cartographie de la Faune (CSCF) and Swiss Entomological Society (SEG).

Ancillotto, L., Labadessa, R., 2024. Functional traits drive the fate of Orthoptera in urban areas. Insect Conserv. Divers. 17, 304–311. https://doi.org/10.1111/icad.12683.

Anderle, M., Paniccia, C., Brambilla, M., Hilpold, A., Volani, S., Tasser, E., Seeber, J., Tappeiner, U., 2022. The contribution of landscape features, climate and topography in shaping taxonomical and functional diversity of avian communities in a heterogeneous Alpine region. Oecologia 199, 499–512. https://doi.org/10.1007/s00442-022-05134-7.

Arbeiter, S., Helmecke, A., Bellebaum, J., 2017. Do Corncrakes *Crex crex* benefit from unmown refuge strips? Bird. Conserv. Int. 27, 560–567. https://doi.org/10.1017/S0959270916000447.

Assandri, G., Bogliani, G., Pedrini, P., Brambilla, M., 2016. Diversity in the monotony? Habitat traits and management practices shape avian communities in intensive vineyards. Agric. Ecosyst. Environ. 223, 250–260. https://doi.org/10.1016/j.agee.2016.03.014.

Assandri, G., Bogliani, G., Pedrini, P., Brambilla, M., 2019. Toward the next Common Agricultural Policy reform: determinants of avian communities in hay meadows reveal current policy's inadequacy for biodiversity conservation in grassland ecosystems. J. Appl. Ecol. 56, 604–617. https://doi.org/10.1111/1365-2664.13332.

Baker, D.J., Freeman, S.N., Grice, P.V., Siriwardena, G.M., 2012. Landscape-scale responses of birds to agri-environment management: a test of the English Environmental Stewardship scheme. J. Appl. Ecol. 49, 871–882. https://doi.org/10.1111/j.1365-2664.2012.02161.x.

Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. https://doi.org/10.1111/cobi.12536.

Batáry, P., Holzschuh, A., Orci, K.M., Samu, F., Tscharntke, T., 2012. Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. Agric. Ecosyst. Environ. 146, 130–136. https://doi.org/10.1016/j.agee.2011.10.018.

Batáry, P., Orci, K.M., Báldi, A., Kleijn, D., Kisbenedek, T., Erdos, S., 2007. Effects of local and landscape scale and cattle grazing intensity on Orthoptera assemblages of the Hungarian Great Plain. Basic Appl. Ecol. 8, 280–290. https://doi.org/10.1016/j.baae.2006.03.012.

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H.G., Lindborg, R., 2019. Grasslands—more important for ecosystem services than you might think. Ecosphere 10, e02582. https://doi.org/10.1002/ecs2.2582.

Bertollo, S., Sommaggio, D., 2012. Riconoscere i Sirfidi: la chiave dicotomica ai generi italiani. Quaderni Della Stazione Di Ecologia Del Civico Museo Di Storia Naturale Di Ferrara. ISSN 0394-5782, pp. 101–145.

Biella, P., Borghesan, S., Colombo, B., Galimberti, A., Guzzetti, L., Maggioni, D., Pioltelli, E., Ramazzotti, F., Ranalli, R., Tommasi, N., Labra, M., 2025. Lawn management promoting tall herbs, flowering species and urban park attributes enhance insect biodiversity in urban green areas. Urban For. Urban Green. 104, 128650. https://doi.org/10.1016/j.ufug.2024.128650.

Bochniak, A., Kulik, M., Jaźwa, M., Sender, J., Ścibior, R., 2024. Evaluation of the mowing frequency effect on floristic diversity of seminatural meadows using generalized diversity indices. Ecol. Indic. 159, 111719. https://doi.org/10.1016/j.ecolind.2024.111719.

Boetzl, F.A., Krauss, J., Heinze, J., Hoffmann, H., Juffa, J., König, S., Krimmer, E., Prante, M., Martin, E.A., Holzschuh, A., Steffan-Dewenter, I., 2021. A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. Proc. Natl. Acad. Sci. 118, e2016038118. https://doi.org/10.1073/pnas.2016038118.

Brambilla, M., Bazzi, G., Ilahiane, L., 2024. The effectiveness of species distribution models in predicting local abundance depends on model grain size. Ecology 105, e4224. https://doi.org/10.1002/ecy.4224.

Braschler, B., Marini, L., Thommen, G.H., Baur, B., 2009. Effects of small-scale grassland fragmentation and frequent mowing on population density and species diversity of orthopterans: a long-term study. Ecol. Entomol. 34, 321–329. https://doi.org/10.1111/j.1365-2311.2008.01080.x.

Buri, P., Arlettaz, R., Humbert, J.Y., 2013. Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: evidence drawn from field-scale experimentation. Agric. Ecosyst. Environ. 181, 22–30. https://doi.org/10.1016/j.agee.2013.09.003.

Cappellari, A., Mei, M., Lopresti, M., Cerretti, P., 2018. Bumblekey: an interactive key for the identification of bumblebees of Italy and Corsica (hymenoptera, apidae). Zookeys 2018 127–138. https://doi.org/10.3897/zookeys.784.25765.

Carmona, C.P., Azcárate, F.M., de Bello, F., Ollero, H.S., Lepš, J., Peco, B., 2012. Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. J. Appl. Ecol. 49, 1084–1093. https://doi.org/10.1111/j.1365-2664.2012.02193.x.

Cavigliasso, P., Phifer, C.C., Knowlton, J.L., Licata, J.A., Flaspohler, D.J., Webster, C.R., Chacoff, N.P., 2022. Influence of landscape composition on wild bee communities: effects of functional landscape heterogeneity. Agric. Ecosyst. Environ. 340, 108150. https://doi.org/10.1016/j.agee.2022.108150.

Cramp, S., 1998. The complete birds of the Western Palearctic. Oxford University Press.

Dalpasso, A., Francesco, G., Calvi, G., Costanzo, A., Falaschi, M., Polidori, C., Rubolini, D., Brambilla, M., 2025. High nature value farmlands to identify crucial agroecosystems for multi-taxa conservation. Biol. Conserv. 305, 111094. https://doi.org/10.1016/j.biocon.2025.111094.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V., 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agric. Ecosyst. Environ. 98, 321–329. https://doi.org/10.1016/S0167-8809(03)00092-6.

de Bello, F., Lavorel, S., Gerhold, P., Reier, Ü., Pärtel, M., 2010. A biodiversity monitoring framework for practical conservation of grasslands and shrublands. Biol. Conserv. 143, 9–17. https://doi.org/10.1016/j.biocon.2009.04.022.

Debastiani, V.J., Pillar, V.D., 2012. SYNCSA-R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics 28, 2067–2068. https://doi.org/10.1093/bioinformatics/bts325.

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of palaearctic grasslands: a synthesis. Agric. Ecosyst. Environ. 182, 1–14. https://doi.org/10.1016/j.agee.2013.12.015.

Drinkwater, E., Robinson, E.J.H., Hart, A.G., 2019. Keeping invertebrate research ethical in a landscape of shifting public opinion. Methods Ecol. Evol. 10, 1265–1273. https://doi.org/10.1111/2041-210X.13208.

Dvoráková, L., Hernová, J., Bušek, O., Reif, J., 2023. Relationships between bird species richness and different facets of landscape heterogeneity - insights from a military area. J. Vertebr. Biol. 72, 23012. https://doi.org/10.25225/jvb.23012.

Estrada-Carmona, N., Sánchez, A.C., Remans, R., Jones, S.K., 2022. Complex agricultural landscapes host more biodiversity than simple ones: a global meta-analysis. Proc. Natl. Acad. Sci. 119, e2203385119. https://doi.org/10.1073/pnas.2203385119.

Ferrari, A., Polidori, C., 2022. How city traits affect taxonomic and functional diversity of urban wild bee communities: insights from a worldwide analysis. Apidologie 53, 46. https://doi.org/10.1007/s13592-022-00950-5.

Fumy, F., Kämpfer, S., Fartmann, T., 2021. Land-use intensity determines grassland Orthoptera assemblage composition across a moisture gradient. Agric. Ecosyst. Environ. 315, 107424. https://doi.org/10.1016/j.agee.2021.107424.

Gagliardi, A., Tosi, G., 2012. Monitoraggio di Uccelli e Mammiferi in Lombardia. Tecniche e metodi di rilevamento. Regione Lombardia, Università degli Studi dell'Insubria. Istituto Oikos.

Grace, J.B., 2006. Structural Equation Modeling and Natural Systems. Cambridge University Press. Cambridge, UK.

Graham, K.K., Graham, K.K., Isaacs, R., Glaum, P., Hartert, J., Tucker, E., Valdovinos, F. S., Glaum, P., Valdovinos, F.S., Glaum, P., Gibbs, J., Tucker, E., Tucker, E., 2024. A century of wild bee sampling: historical data and neural network analysis reveal ecological traits associated with species loss. Proc. R. Soc. B Biol. Sci. 291, 20232837. https://doi.org/10.1098/rspb.2023.2837.

Granata, E., Assandri, G., Franzoi, A., Pedrini, P., Brambilla, M., 2025. Management, topography and landscape contribute to shape bird communities in Alpine semi-natural grasslands. Biol. Conserv. 311, 111409. https://doi.org/10.1016/j.biocon.2025.111409.

Guerra, J.G., Cabello, F., Fernández-Quintanilla, C., Peña, J.M., Dorado, J., 2022. Plant functional diversity is affected by weed management through processes of trait convergence and divergence. Front. Plant Sci. 13, 993051. https://doi.org/10.3389/fpls.2022.993051.

Halassy, M., Botta-dukát, Z., Csecserits, A., Szitár, K., Török, K., 2019. Trait-based approach confirms the importance of propagule limitation and assembly rules in old-field restoration. Restor. Ecol. 27, 840–849. https://doi.org/10.1111/rec.12929.

Hassan, N., Zhong, Z., Wang, D., Zhu, Y., Naeen, I., Ahungu, A.B., Wan, H.Y., Li, X., 2023. Effects of long-term mowing on species diversity, biomass and composition of plant community in a semi-arid grassland in northeastern China. Appl. Veg. Sci. 26, e12743. https://doi.org/10.1111/avsc.12743.

Hejcman, M., Hejcmanová, P., Pavlů, V., Beneš, J., 2013. Origin and history of grasslands in central europe - a review. Grass Forage Sci. 68, 345–363. https://doi.org/10.1111/gfs.12066.

Humbert, J.Y., Ghazoul, J., Richner, N., Walter, T., 2012. Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. Biol. Conserv. 152, 96–101. https://doi.org/10.1016/j.biocon.2012.03.015.

Iorio, C., Scherini, R., Fontana, P., Buzzetti, F.M., Kleukers, R., Odè, B., Massa, B., 2019. Grasshoppers and crickets of Italy. A photographic field guide to all the species. WBA books.

Jiao, S., Peng, Z., Qi, J., Gao, J., Wei, G., 2021. Linking bacterial-fungal relationships to microbial diversity and soil nutrient cycling. e01052-20 mSystems 6. https://doi.org/10.1128/msystems.01052-20.

Kaláb, O., Šipoš, J., Kočárek, P., 2020. Leaving uncut refuges during meadow harvesting increases the functional diversity of Orthoptera. Entomol. Sci. 23, 95–104. https://doi.org/10.1111/ens.12404.

Kent, M., 2011. Vegetation Description and Data Analysis: A Practical Approach, second Ed. Wiley-Blackwell.

Klaus, F., Ayasse, M., Classen, A., Dauber, J., Diekötter, T., Everaars, J., Fornoff, F., Greil, H., Hendriksma, H.P., Jütte, T., Klein, A.M., Krahner, A., Leonhardt, S.D., Lüken, D.J., Paxton, R.J., Schmid-Egger, C., Steffan-Dewenter, I., Thiele, J., Tscharntke, T., Erler, S., Pistorius, J., 2024. Improving wild bee monitoring, sampling methods, and conservation. Basic Appl. Ecol. 75, 2–11. https://doi.org/10.1016/j.baae.2024.01.003.

Krebs, C.J., 1999. Ecological Methodology, 2nd ed. Benjamin/Cummings, Menlo Park.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R. Packag. Version 1, 0-12.3.

Larkin, M., Stanley, D.A., 2021. Impacts of management at a local and landscape scale on pollinators in semi-natural grasslands. J. Appl. Ecol. 58, 2505–2514. https://doi.org/10.1111/1365-2664.13990.

Larsson, M., Franzén, M., 2008. Estimating the population size of specialised solitary bees. Ecol. Entomol. 33, 232–238. https://doi.org/10.1111/j.1365-2311.2007.00956.x.

Lauber, K., Wagner, G., 1998. Flora Helvetica. Haupt Verlag, Bern.

Lezzeri, M., Lozano, V., Brundu, G., Floris, I., Pusceddu, M., Quaranta, M., Satta, A., 2024. Standardized transect walks outperform pan traps in assessing wild bee community in a Mediterranean protected area (Asinara National Park, Italy). Biodivers. Conserv. 33, 1–16. https://doi.org/10.1007/s10531-024-02850-9.

Löffler, F., Fartmann, T., 2017. Effects of landscape and habitat quality on Orthoptera assemblages of pre-alpine calcareous grasslands. Agric. Ecosyst. Environ. 248, 71–81. https://doi.org/10.1016/j.agee.2017.07.029.

Marsoner, T., Simion, H., Giombini, V., Vigl, L.E., Candiago, S., 2023. A detailed land use/land cover map for the European Alps macro region. Sci. Data 10, 468. https://doi.org/10.1038/s41597-023-02344-3.

Massa, B., Fontana, P., Buzzetti, F.M., Kleukers, R., Odè, B., 2012. Fauna d'Italia vol. XLVIII - Orthoptera, Calderini. ed. Bologna, Italy.

Mercuri, A.M., Florenzano, A., Clò, E., Braga, L., Zappa, J., Cremaschi, M., Zerboni, A., 2025. The precision land knowledge of the past enables tailor-made environment therapy and empathy for nature. Sci. Rep. 15, 12587. https://doi.org/10.1038/s41598-025-97372-x.

Meyer, S., Unternährer, D., Arlettaz, R., Humbert, J.Y., Menz, M.H.M., 2017. Promoting diverse communities of wild bees and hoverflies requires a landscape approach to managing meadows. Agric. Ecosyst. Environ. 239, 376–384. https://doi.org/10.1016/j.agee.2017.01.037.

Michez, D., Rasmont, P., Terzo, M., Vereecken, N., 2019. Bees of Europe. Hymenoptera of Europe. NAP Editions.

Michez, D., Terzo, M., Rasmont, P., 2004. Révision des espèces ouest-paléarctiques du genre Dasypoda Latreille 1802 (Hymenoptera, Apoidea, Melittidae). Linz. Biol. Beitr. äge 36, 847–900.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004.

Mudrák, O., Janeček, Š., Götzenberger, L., Mason, N.W.H., Horník, J., de Castro, I., Doležal, J., Klimešová, J., de Bello, F., 2016. Fine-scale coexistence patterns along a productivity gradient in wet meadows: Shifts from trait convergence to divergence. Ecography 39, 338–348. https://doi.org/10.1111/ecog.01723.

Muñoz-Sáez, A., Kitzes, J., Merenlender, A.M., 2021. Bird-friendly wine country through diversified vineyards. Conserv. Biol. 35, 274–284. https://doi.org/10.1111/cobi.13567.

Nodari, A.M., Bonifacino, M., Eustacchio, E., Bonelli, M., Falaschi, M., 2025. Comparing sampling methods to monitor population abundance while accounting for imperfect detection: an application of *N*-mixture models on Orthoptera. Glob. Ecol. Conserv. 58, e03435. https://doi.org/10.1016/j.gecco.2025.e03435.

Noordijk, J., Delille, K., Schaffers, A.P., Sýkora, K.V., 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biol. Conserv. 142, 2097–2103. https://doi.org/10.1016/j.biocon.2009.04.009.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, K., 2022. vegan: Community ecology package. R package version 2, pp. 6–7.

Oyarzabal, G., Guimarães, M., 2021. Friend and foe? The effects of grassland management on global patterns of spider diversity. Ecol. Entomol. 46, 1195–1204. https://doi.org/10.1111/een.13065.

Pankiv, K., Kloetzer, L., 2024. Does using artificial intelligence in citizen science support volunteers' learning? An experimental study in ornithology. Citiz. Sci. Theory Pr. 9, 36. https://doi.org/10.5334/cstp.733.

Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbé, A., Wulf, F., Scott, A.V., 2014. EU agricultural reform fails on biodiversity. Science 344, 1090–1092. https://doi.org/10.1126/science.1253425.

Petermann, J.S., Buzhdygan, O.Y., 2021. Grassland biodiversity. Curr. Biol. 31, R1195–R1201. https://doi.org/10.1016/j.cub.2021.06.060.

Phukubye, K., Mutema, M., Buthelezi, N., Muchaonyerwa, P., Cerri, C., Chaplot, V., 2022. On the impact of grassland management on soil carbon stocks: a worldwide meta-analysis. Geoderma Reg. 28, e00479. https://doi.org/10.1016/j.geodrs.2021.e00479.

Piano, E., Isaia, M., Falasco, E., La Morgia, V., Soldato, G., Bona, F., 2017. Local versus landscape spatial influence on biodiversity: a case study across five European industrialized areas. Environ. Monit. Assess. 189, 126. https://doi.org/10.1007/s10661-017-5824-7.

Pignatti, S., Guarino, R., La Rosa, M., 2007. Flora d'Italia. Edagricole-New Business Media.

Pillay, R., Fletcher, R.J., Sieving, K.E., Udell, B.J., Bernard, H., 2019. Bioacoustic monitoring reveals shifts in breeding songbird populations and singing behaviour with selective logging in tropical forests. J. Appl. Ecol. 56, 2482–2492. https://doi.org/10.1111/1365-2664.13492.

Poos, M.S., Jackson, D.A., 2012. Addressing the removal of rare species in multivariate bioassessments: the impact of methodological choices. Ecol. Indic. 18, 82–90. https://doi.org/10.1016/j.ecolind.2011.10.008.

Popic, T.J., Davila, Y.C., Wardle, G.M., 2013. Evaluation of common methods for sampling invertebrate pollinator assemblages: net sampling out-perform pan traps. PLoS One 8, e66665. https://doi.org/10.1371/journal.pone.0066665.

Potts, S.G., Bartomeus, I., Biesmeijer, K., Breeze, T., Casino, A., Dauber, J., Dieker, P., Hochkirch, A., Høye, T., Isaac, N., Kleijn, D., Laikre, L., Mandelik, Y., Montagna, M., Montero Castaño, A., Öckinger, E., Oteman, B., Pardo Valle, A., Polce, C., Povellato, A., Quaranta, M., Roy, D., Schweiger, O., Settele, J., Ståhls-Mäkelä, G., Tamborra, M., Troost, G., van der Wal, R., Vujić, A., Zhang, J., 2024. Refined proposal for an EU pollinator monitoring scheme. Publications Office of the European Union.

Prangel, E., Kasari-Toussaint, L., Neuenkamp, L., Noreika, N., Karise, R., Marja, R., Ingerpuu, N., Kupper, T., Keerberg, L., Oja, E., Meriste, M., Tiitsaar, A., Ivask, M., Helm, A., 2023. Afforestation and abandonment of semi-natural grasslands lead to biodiversity loss and a decline in ecosystem services and functions. J. Appl. Ecol. 60, 825–836. https://doi.org/10.1111/1365-2664.14375.

Proske, A., Lokatis, S., Rolff, J., 2022. Impact of mowing frequency on arthropod abundance and diversity in urban habitats: a meta-analysis. Urban For. Urban Green. 76, 127714. https://doi.org/10.1016/j.ufug.2022.127714.

Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S.G., Durka, W., Kühn, I., Winter, M., Prentice, H.C., 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. J. Ecol. 101, 857–866. https://doi.org/10.1111/1365-2745.12098.

R Core Team, 2023. R: A language and environment for statistical computing. R Found. Stat. Comput.

Rahman, M.M., Zimmer, M., Ahmed, I., Donato, D., Kanzaki, M., Xu, M., 2021. Co-benefits of protecting mangroves for biodiversity conservation and carbon storage. Nat. Commun. 12, 3875. https://doi.org/10.1038/s41467-021-24207-4.

Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. Theor. Popul. Biol. 21, 24–43. https://doi.org/10.1016/0040-5809(82)90004-1.

Révész, K., Gallé, R., Humbert, J.Y., Batáry, P., 2025. Effects of uncut refuge management on grassland arthropods – a systematic review. Glob. Ecol. Conserv. 57, e03381. https://doi.org/10.1016/j.gecco.2024.e03381.

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98, 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x.

Rosseel, Y., 2012. lavaan: An R package for structural equation modeling. J. Stat. Softw. 48, 1–36. https://doi.org/10.18637/jss.v048.i02.

Rossier, L.C.P., Auberson, C., Arlettaz, R., Humbert, J.Y., 2023. Effects of uncut grass refuges on the plant community of extensively managed hay meadows. Basic Appl. Ecol. 72, 38–44. https://doi.org/10.1016/j.baae.2023.07.003.

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. Ecol. Lett. 16, 912–920. https://doi.org/10.1111/ele.12128.

Schermelleh-Engel, K., Moosbrugger, H., Müller, H., 2003. Evaluating the fit of structural equation models: tests of significance and descriptive goodness-of-fit measures. Methods Psychol. Res. 8, 23–74. https://doi.org/10.23668/psycharchives.12784.

Shapiro, S., Wilk, M., 1965. An analysis of variance test for normality (Complete Samples). Biometrika 52, 591–611. https://doi.org/10.1093/biomet/52.3-4.591.

Silva, C.P., García, C.E., Estay, S.A., Barbosa, O., Chapman, M.G., 2015. Bird richness and abundance in response to urban form in a Latin American City: Valdivia, Chile as a Case Study. PLoS One 10, e0138120. https://doi.org/10.1371/journal.pone.0138120.

Simons, N.K., Weisser, W.W., Gossner, M.M., 2016. Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. Ecology 97, 754–764. https://doi.org/10.1890/15-0616.

Stephens, L., Fuller, D., Boivin, N., Rick, T., Gauthier, D., Kay, A., Marwick, B., Geralda, C., Armstrong, D., Barton, C., Dnham, T., Douglass, K., Driver, J., Janz, L., Roberts, P., Rogers, J., Thakar, H., Altawee, M., Johnson, A., Sampietro Vattuone, M., Aldenderfer, M., Archila, S., Artioli, G., Bale, M., Beach, T., Borrell, F., Braje, T., Buckland, P.I., Jiménez Cano, N.G., Capriles, J.M., Diez Castillo, A., Çilingiroglu, Ç., Negus Cleary, M., Conolly, J., Coutros, P., Covey, A., Cremaschi, M., Crowther, A., Der, L., di Lernia, S., Doershuk, J., Doolittle, W.E., Edwards, K.J., Erlandson, J., Evans, D., Faribairn, A., Faulkner, P., Feinman, G., Fernandes, R., Fitzpatrick, S., Fyfe, R., Garcea, E., Goldstein, S., Goodman, R., Dalpoim Guedes, J., Herrmann, J., Hiscock, P., Hommel, P., Horsburgh, K., Hritz, C., Ives, J., Junno, A., Khan, J., Kaufman, B., Kearns, C., Kidder, T., Lanoë, F., Lawrence, D., Lee, G., Levin, M.L., Lindskoug, H., López-Sáez, J., Macrae, S., Marchant, R., Marston, J., McClure, S., McCoy, M., Ventresca Miller, A., Morrison, G., Matuzeviciute, G., Muller, J., Nayak, A., Noerwidi, S., Peres, T., Crowther, C., Proctor, L., Randall, A., Renette, S., Robbins Schug, G., Ryzewski, K., Saini, R., Sceinsohn, V., Schmidt, P., Sebillaud, P., Seitsonen, O., Simpson, I., Soltysiak, A., Speakman, R., Spengler, R., Steffen, M., Storozum, M., Strickland, K., Thomposon, J., Thurston, T., Ulm, S., Ustunkaya, M., Welker, M., West, C., Ryan Williams, P., Wright, D., Wright, N., Zahir, M., Zerboni, A., Beadoin, E., Munevar Garcia, S., Powell, J., Thornton, A., Kaplan, J., Gaillard, M., Klein Goldewijk, K., Ellis, E., 2019. Archaeological assessment reveals Earth's early transformation through land use. Science 902 (80), 897–902. https://doi.org/10.1126/science.aax1192.

Stoch, F., Genovesi, P., 2016. Manuali per il monitoraggio di specie e habitat di interesse comunitario (Direttiva 92/43/CEE) in Italia: specie animali. ISPRA.

Sugai, L.S.M., Silva, T.S.F., Ribeiro, J.W., Llusia, D., 2019. Terrestrial passive acoustic monitoring: review and perspectives. BioScience 69, 15–25. https://doi.org/10.1093/biosci/biy147.

Sutherland, W.J., 2006. In: Handbook, A. (Ed.), Ecological Census Techniques. Cambridge University Press.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., Milberg, P., 2016. Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. Agric. Ecosyst. Environ. 222, 200–212. https://doi.org/10.1016/j.agee.2016.02.008.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., Milberg, P., 2018. Similar effects of different mowing frequencies on the conservation value of semi-natural grasslands in Europe. Biodivers. Conserv. 27, 2451–2475. https://doi.org/10.1007/s10531-018-1562-6.

Toikkanen, J., Halme, P., Kahanpää, J., Toivonen, M., 2022. Effects of landscape composition on hoverflies (Diptera: Syrphidae) in mass-flowering crop fields within forest-dominated landscapes. J. Insect Conserv. 26, 907–918. https://doi.org/10.1007/s10841-022-00436-w.

Torma, A., Császár, P., Bozsó, M., Deák, B., Valkó, O., Kiss, O., Gallé, R., 2019. Species and functional diversity of arthropod assemblages (Araneae, Carabidae, Heteroptera and Orthoptera) in grazed and mown salt grasslands. Agric. Ecosyst. Environ. 273, 70–79. https://doi.org/10.1016/j.agee.2018.12.004.

Van Veen, M., 2004. Hoverflies of Northwest Europe: identification keys to the Syrphidae. KNNV Publishing, Utrecht.

Wang, L., Delgado-Baquerizo, M., Wang, D., Isbell, F., Liu, Jun, Feng, C., Liu, Jushan, Zhong, Z., Zhu, H., Yuan, X., Chang, Q., Liu, C., 2019. Diversifying livestock promotes multidiversity and multifunctionality in managed grasslands. Proc. Natl. Acad. Sci. 116, 6187–6192. https://doi.org/10.1073/pnas.1807354116.

Wenzel, A., Grass, I., Raj, V., Nölke, N., Subramanya, S., Tscharntke, T., 2023. High losses of farmland birds and potential biocontrol along an urbanization gradient in a tropical megacity. Agric. Ecosyst. Environ. 354, 108571. https://doi.org/10.1016/j.agee.2023.108571.

Werling, B.P., Dickson, T.L., Isaacs, R., Gaines, H., Gratton, C., Gross, K.L., Liere, H., Malmstrom, C.M., Meehan, T.D., Ruan, L., Robertson, B.A., Robertson, G.P., Schmidt, T.M., Schrotenboer, A.C., Teal, T.K., Wilson, J.K., Landis, D.A., 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. Proc. Natl. Acad. Sci. 111, 1652–1657. https://doi.org/10.1073/pnas.1309492111.

Westland, J.C., 2019. Structural Equation Models - From paths to networks, Second edi. ed. Springer Nature.

Wider, S., Zemp, D.C., 2025. Bird and hoverfly communities are impacted by vegetation heterogeneity in wood-pastures in the Swiss Jura. Biodivers. Conserv. 34, 2139–2162. https://doi.org/10.1007/s10531-025-03066-1.

Wu, L., Chen, H., Chen, D., Wang, S., Wu, Y., Wang, B., Liu, S., Yue, L., Yu, J., Bai, Y., 2023. Soil biota diversity and plant diversity both contributed to ecosystem stability in grasslands. Ecol. Lett. 26, 858–868. https://doi.org/10.1111/ele.14202.