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Wetlands lead, but all ecosystems matter: quantifying conservation priorities for plant communities in agricultural landscapes

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ABSTRACT

Agricultural landscapes are mosaics of different ecosystem types, each hosting distinct plant communities. Despite the known role of ecosystem diversification in sustaining farmland biodiversity, quantitative large-scale assessments of how different plant communities contribute to overall biodiversity within these landscapes remain limited. Here, we identified conservation priorities for plant communities across multiple ecosystem types in agricultural landscapes by quantifying their contributions to plant diversity. We sampled vegetation in croplands, forests, grasslands, shrublands, and wetlands across 46 study sites in Italy using 230 quadrats of 25 m^2. We tested differences in plant community α-diversity, β-diversity, and species composition using multiple complementary metrics. Grasslands exhibited the highest species richness, whereas wetlands showed the lowest. However, wetlands displayed the highest Local Contribution to Beta Diversity (LCBD), reflecting their distinctive species composition. Wetland and woody species exhibited the highest Species Contribution to Beta Diversity (SCBD). Grasslands hosted the highest number of unique species, whereas wetlands showed the highest proportion of unique species. Although the number and proportion of red-listed species did not differ significantly among ecosystem types, wetlands consistently exhibited higher values. Croplands and grasslands were the richest in non-native species; however, invasion levels remained low across the dataset. Species composition differed significantly among all ecosystem types. Based on the assessed metrics, wetlands had the highest conservation priority for vascular plant diversity. However, all ecosystem types contributed to the conservation of unique plant species and communities. Maximizing vascular plant diversity therefore requires maintaining diversified agricultural landscapes integrating different ecosystem types within a spatially connected mosaic.

1. Introduction

Agricultural landscapes are mosaics of different ecosystem patches, such as croplands, forests, grasslands, shrublands, and wetlands, each supporting distinct plant communities (Landis, 2017). Shaped by the interplay between environmental processes and long-term human activities, some may sustain biodiversity levels comparable to, or even exceeding, those of less managed landscapes (Benton et al., 2003; Strohbach et al., 2015). Particularly where agriculture dominates land use, increased landscape heterogeneity has been widely associated with higher multi-taxonomic species richness and abundance (Fahrig et al., 2011; Priyadarshana et al., 2024). Such heterogeneity largely results from the superimposition of agro-silvo-pastoral activities onto pre-existing unmanaged landscapes, which can generate novel ecological niches and increase biodiversity (Mueller et al., 2021). By integrating diverse ecosystems within limited spatial extents, agricultural landscapes can therefore support species and communities associated with gradients of management intensity and environmental conditions (Tscharntke et al., 2005). Maintaining and restoring diverse ecosystems across agricultural landscapes is important for biodiversity conservation in farmlands, as it supports higher biodiversity than applying sustainable practices in homogeneous landscapes (Tscharntke et al., 2021).

Understanding the extent to which different ecosystem types contribute to overall biodiversity is important to define appropriate conservation and management strategies since certain ecosystems contribute disproportionately to landscape biodiversity (Harper et al., 2022). Wetlands often support distinctive species and communities despite their limited spatial extent and reduced species richness (Mitsch and Gosselink, 2000; Richardson et al., 2015; Cannucci et al., 2025). Grasslands and shrublands provide refuges for species sensitive to land-use intensification and make an important contribution to landscape-scale biodiversity (Batáry et al., 2011; Fanfarillo et al., 2023a). Forest fragments embedded within agricultural matrices enhance habitat continuity and connectivity for forest-dependent species (Fahrig, 2003). Extensively managed agroecosystems such as traditional arable systems or centuries-old olive groves hold substantial conservation value as well (Janssen et al., 2016; Casavecchia et al., 2021; Fanfarillo and Kasperski, 2021). Such evidence highlights the need to quantify the levels of biodiversity that different ecosystems can sustain across taxonomic groups.

European landscapes have been shaped by agro-silvo-pastoral practices over millennia (Santoro, 2024), contributing to maintaining the mosaic of forested and open habitats that characterized the continent till the extinction of megafauna (Czyżewski et al., 2026). European extensive, traditional agricultural areas are commonly referred to as High Nature Value farmlands (HNVFs). High Nature Value (HNV) farming denotes low-intensity agricultural practices that support elevated biodiversity levels while maintaining ecosystems and habitats of conservation concern (Oppermann et al., 2012). Such systems are typically characterized by extensive land use, low chemical inputs, and the presence of structurally diversified vegetation, which collectively favour the persistence of species and communities declining in intensively managed landscapes (Beaufoy and Cooper, 2008). Investigating the diversity of plant communities in agricultural landscapes is crucial to identify HNVFs, given the importance of vegetation in shaping habitats, ecosystems, and landscape features (Maskell et al., 2019; Bagella et al., 2020). HNVFs are increasingly threatened by both land-use intensification and land abandonment, both causing a decrease in landscape heterogeneity and biodiversity, compared to areas shaped by traditional low-intensity farming (Foley et al., 2005; Falcucci et al., 2007; Strohbach et al., 2015; Fanfarillo et al., 2019a, 2023a).

In agricultural landscapes, vascular plants provide a suitable model for assessing biodiversity patterns and conservation priorities. As primary producers, they are at the base of ecosystem functioning, constitute a substantial component of the total biodiversity, and support other taxonomic groups by providing trophic resources and acting as ecosystem engineers (Losapio et al., 2021). Quantifying the contribution of different plant communities to the total plant diversity is therefore important for identifying conservation priorities and informing sustainable land-use management that reconciles agricultural production with biodiversity conservation (Foley et al., 2005). For prioritization purposes, simple biodiversity metrics such as species richness or Shannon diversity may fail to capture important aspects of conservation value (Fleishman et al., 2006; Capmourteres and Anand, 2016; Fiaschi et al., 2023). For instance, high species richness may reflect human

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disturbance, favouring generalist or invasive species at the expense of specialists and natives (McKinney and Lockwood, 1999; Fanfarillo et al., 2024a). The analysis of β-diversity, defined as the variation in species composition, richness, and abundance among sites (Whittaker, 1960), may help overcome these limitations. By capturing biodiversity uniqueness and complementarity, β-diversity clarifies how species and communities from different ecosystem types contribute to regional biodiversity (Anderson et al., 2011; Fanfarillo et al., 2023b; Pafumi et al., 2024). High β-diversity levels indicate that different sites host different communities that collectively enhance landscape-scale biodiversity (Legendre and De Cáceres, 2013).

β-diversity can be partitioned into replacement and richness difference. Species replacement describes the substitution of species along ecological gradients and depends on species' ecological tolerance or niche breadth, whereas richness difference denotes variation in species number between communities and may reflect differences in available niches across locations (Legendre, 2014). Furthermore, β-diversity can be decomposed into the contributions of individual communities and species. Local Contribution to Beta Diversity (LCBD) quantifies the extent to which each community contributes to total β-diversity. High LCBD values indicate communities with species compositions that are distinct from those of other communities, resulting from the presence of unique species and/or from unique species associations. Species Contribution to Beta Diversity (SCBD) measures the contribution of each species to total β-diversity, identifying those that most strongly differentiate communities through their occurrence or abundance (Legendre and De Cáceres, 2013). In conservation studies, these metrics help identify the communities and species that contribute disproportionately to landscape-scale biodiversity and complementarity, thereby supporting conservation prioritization. However, high LCBD or SCBD values do not necessarily indicate high conservation value, as they may reflect either unique communities and species of conservation value or degraded communities characterized by disturbance-tolerant or non-native species. Their interpretation therefore requires integration with information on species composition and species ecology (Legendre and De Cáceres, 2013; Legendre, 2014).

Despite the recognized importance of ecosystem heterogeneity and plant community diversification in farmlands, quantitative assessments of the relative contribution of different plant communities to biodiversity in agricultural landscapes remain limited and have often been conducted at local spatial scales (Gabriel et al., 2006; Lindborg et al., 2014). Previous studies have examined animal groups, individual habitat types, natural areas, or specific management practices (de Snoo et al., 2012; Wu et al., 2018). However, integrated assessments encompassing multiple ecosystem types within agricultural landscapes remain relatively uncommon (Tscharntke et al., 2012). Furthermore, many investigations emphasize patterns of species richness and abundance, whereas fewer explicitly address species composition and β-diversity, which are fundamental for understanding community uniqueness and complementarity (Legendre and De Cáceres, 2013; Draper et al., 2018; Fanfarillo et al., 2023b).

Within this framework, the present study aims to identify conservation priorities for plant communities across different ecosystem types in Italian agricultural landscapes by quantifying the contributions of these communities to α-diversity, β-diversity, and γ-diversity, as well as their role in sustaining unique and red-listed plant species. By doing so, we aim to improve understanding of how ecosystem diversity promotes plant diversity at large geographic scales and to provide evidence-based insights that support land-use strategies balancing agricultural productivity with biodiversity conservation through the design of sustainable agricultural landscapes.

2. Materials and methods

2.1. Study area

Italy is located in southern Europe, approximately at the centre of the Mediterranean Basin (WGS84: 35–47° N, 6–18° E; Fig. 1). Most of its territory consists of the Apennine Peninsula, which extends across the central and southern parts of the country. The northern continental sector is bounded by the Alps to the north and includes the extensive Po–Venetian Plain. The insular component comprises the two major islands, Sardinia and Sicily, together with several archipelagos and minor islands. Much of the territory is characterized by hilly and mountainous landscapes, particularly in central and southern Italy and on the islands, whereas the northern sector is largely occupied by the Po and Venetian plains, forming the largest alluvial lowland in the country. Elevation ranges from −3 m a.s.l. near the Po Delta to 4805 m a.s.l. at Monte Bianco. The highly complex geomorphological setting and relevant latitudinal extent give rise to pronounced climatic heterogeneity, with Mediterranean and temperate macrobioclimates representing the two dominant types, distinguished by the presence or absence of summer drought, respectively; the Temperate macrobioclimate further includes a submediterranean variant and a steppic variant (Pesaresi et al., 2017).

Italy also exhibits a complex geological framework shaped by the interaction between the African and Eurasian plates, resulting in a heterogeneous mosaic of substrates, including carbonate platforms, flysch sequences, volcanic districts, metamorphic and igneous units, and extensive alluvial deposits (ISPRA, 1990 onwards). This geological diversity underlies an equally varied soil system, with Cambisols, Luvisols, Leptosols, Andosols, Vertisols, and Calcisols widely distributed across different geomorphological contexts (Costantini et al., 2012; Costantini and Dazzi, 2013). The combination of heterogeneous morphoclimatic

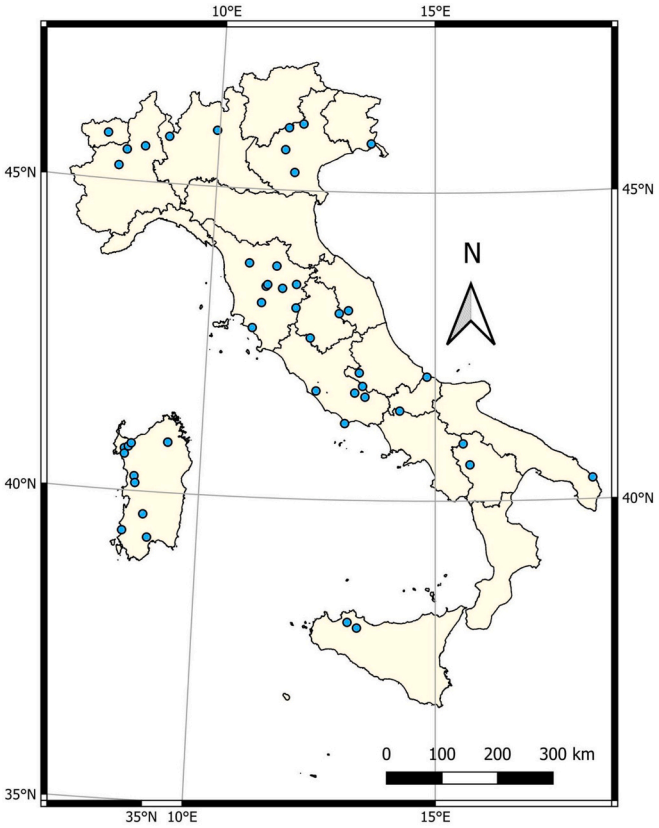

Fig. 1. – Location of the study sites within Italy. Black lines indicate the boundaries of administrative regions. Coordinates: WGS84 (EPSG: 4326).

conditions and a long history of human land use has generated a high diversity of vegetation types across the country (Blasi et al., 2010). Italian agricultural landscapes exhibit high diversification after long-term human land use interacting with heterogeneous topography and climate (Zavattero et al., 2021). Moreover, the intensification of agricultural practices on the one hand and land abandonment on the other have caused marked changes in Italian farmland plant diversity, including a reduction in the extent of traditional agricultural areas that previously supported numerous species and communities (Fanfarillo et al., 2019a, 2019b). Sustainable management of these landscapes is therefore important not only for agricultural production but also for biodiversity conservation in a country largely included within one of the world's biodiversity hotspots (Myers et al., 2000).

2.2. Data collection

In the first months of 2023, we launched a call inviting expert botanists to collect plant community data in agricultural landscapes, each used as a study site. The selection of study sites therefore depended on the participation and availability of collaborators. Participating botanists preferentially selected agricultural landscapes that contained five target ecosystem types. This collaborative sampling strategy resulted in the selection of 46 study sites distributed across Italy (Fig. 1). Each study site was delineated by a circular buffer with a radius of 1 km to standardize the spatial extent of the study sites and to ensure that all sampled ecosystem types belonged to the same local landscape context. A similar spatial extent has been adopted in previous studies on plant diversity in agricultural mosaics (Pallavicini et al., 2020). Within each study site, we sampled one plant community for each of the following broad ecosystem types, which were defined according to vegetation structure as well as associated environmental and management conditions:

1. Croplands: including any type of annual or perennial crop;
2. Grasslands: encompassing pastures, meadows, and ruderal grasslands, with negligible shrub and tree cover (< 10%);
3. Shrublands: dominated by a shrub layer 1–3 m high, covering at least 80% of the plot surface;
4. Forests: dominated by a tree layer >3 m high, covering at least 80% of the plot surface;
5. Wetlands: characterized by still or flowing water at least 5 cm deep, covering at least 80% of the plot surface.

Such cover and height thresholds were adopted as operational criteria to ensure that plots were consistently assigned to the target ecosystem types and to minimize overlap among transitional communities. Hereafter, we use the terms croplands, grasslands, shrublands, forests, and wetlands to refer to the plant communities sampled within these ecosystem types. The location of each plot was selected preferentially in the field based on the presence of ecosystem patches with the required characteristics. We sampled plant communities using square plots of 25 m^2. Within each plot, we recorded all vascular plant species present and visually estimated their percentage cover using the following scale: 0.1, 0.2, and 0.5%; 1–10% at 1% intervals; and 10–100% at 5% intervals. Finer intervals were used at low cover values to improve resolution for less abundant species, whereas broader intervals were used at higher cover values to account for the decreasing precision of visual cover estimates as cover increases (Klimeš, 2003; Vittoz and Guisan, 2007). Direct percentage estimates also avoid the information loss associated with ordinal cover scales and are recommended when quantitative cover data are used in subsequent analyses (Dembicz and Dengler, 2025). We also recorded total vegetation cover, mean vegetation height, aspect, slope, water depth (in wetlands), and plot coordinates. We surveyed a total of 230 plots. Plant taxa were identified at the species level according to Pignatti et al. (2017–2019), and taxonomic nomenclature followed World Flora Online (Borsch et al., 2020).

2.3. Diversity metrics calculation

Prior to all calculations and analyses, we removed crop species from cropland plots to avoid masking diversity patterns in wild plant communities. For each plot, we calculated species richness as a measure of α-diversity. Dissimilarity-based β-diversity and its components (replacement and richness difference) were calculated using the function *beta.div.comp* in the R package *adespatial* (Dray et al., 2023; R Core Team, 2024), adopting the Jaccard coefficient as the distance measure. Variance-based β-diversity, Local Contributions to Beta Diversity (LCBDs), and Species Contributions to Beta Diversity (SCBDs) were calculated using the function *beta.div* in the same package after Hellinger transformation of species abundances. In addition, we identified species occurring exclusively within a single ecosystem type by pooling all plots belonging to the same ecosystem type and comparing the resulting species lists across ecosystem types. For each plot, we calculated the number and percentage of species that were unique to the corresponding ecosystem type relative to the total number of species recorded in the plot. We also calculated, for each plot, the number and percentage of species included in the Italian Red List (Orsenigo et al., 2018, 2021), excluding species classified as “Least Concern” or “Data Deficient”, and the number and percentage of non-native species, using species classified as non-native at the national scale (Portal to the Flora of Italy, 2025). Since the sampling design was balanced, with the same number of plots ($n = 46$) for each ecosystem type, we quantified the contribution of each ecosystem type to total variance-based β-diversity by summing the LCBD values of its plots. Because LCBD values represent the relative contribution of individual plots to total variance-based β-diversity and sum to one across all plots (Legendre and De Cáceres, 2013), the summed LCBD values represent the relative contribution of each ecosystem type. These values were multiplied by 100 for graphical representation.

2.4. Univariate statistical analyses

We tested for differences among ecosystem types in plant community species richness, LCBD, number and percentage of unique species, number and percentage of red-listed species, and number and percentage of non-native species using the Scheirer–Ray–Hare test (*scheirerRayHare* function, *rcompanion* package; Mangiafico, 2024). This non-parametric approach was adopted because none of the response variables met the assumptions of normality and homoscedasticity required by parametric models, as assessed using Shapiro–Wilk tests (*shapiro.test* function, *stats* package - R Core Team, 2024). Because the sampling design included one plot per ecosystem type within each of the 46 study sites, plots from the same area could not be considered independent. We therefore included both ecosystem type and study site as independent variables in the Scheirer–Ray–Hare tests, allowing us to account for variation among study sites while testing for differences among ecosystem types. When a significant effect of ecosystem type was detected, we performed post hoc pairwise comparisons using Dunn's test (*dunn_test* function, *rstatix* package; Kassambara, 2025) with Holm adjustment for multiple comparisons.

2.5. Multivariate statistical analyses

Differences in plant species composition among the five ecosystem types were analysed using Permutational Multivariate Analysis of Variance (PERMANOVA), performed in PRIMER v.7 (Clarke et al., 2014), based on a Bray-Curtis distance matrix after log(x + 1) transformation of species cover values to reduce the influence of highly dominant species. The model included ecosystem type as a fixed factor and study site as a random factor, thereby accounting for the hierarchical structure of the data. When a significant effect of ecosystem type

was detected, pairwise comparisons among ecosystem types were performed using the pairwise permutation tests implemented in PERMANOVA+ (PRIMER v.7), based on pseudo-*t* statistics and 999 permutations. To visualize patterns in species composition, we performed a non-metric multidimensional scaling (NMDS) ordination using the function *metaMDS* in the *vegan* package. Ordination was based on Bray–Curtis dissimilarities calculated on log(x + 1)-transformed species cover data (Anderson, 2001).

3. Results

3.1. Study sites

We surveyed 44 sites during the 2023 growing season and two sites during the 2024 growing season. The study sites encompassed highly diverse agricultural landscapes, ranging from lowland intensive systems to extensive agricultural areas in hills and mountains. The sites were distributed between 37.9° and 46.1° N and between 7.4° and 18.3° E, at elevations between 1 and 958 m a.s.l. Twenty-one sites had a Mediterranean macrobioclimate, whereas 25 sites had a Temperate macrobioclimate. Among the latter, one site had a Temperate steppic bioclimate and 13 sites had a Temperate submediterranean bioclimate (Pesaresi et al., 2017). Soil types were highly heterogeneous, spanning 20 different soil provinces (Costantini et al., 2012). Full details for each study site are provided in Appendix A.

3.2. Patterns of α and β-diversity

Significant differences were observed in species richness, LCBD, and the number and percentage of unique and non-native species among the plant communities of the five ecosystem types. Conversely, no significant differences were detected in the number or percentage of red-listed species, although wetlands exhibited higher values for both (Table 1, Fig. 2).

The plant communities exhibited a total dissimilarity-based β-diversity of 0.49, with a replacement component of 0.29 (59.18%) and a richness difference component of 0.20 (40.82%) (Fig. 2a). Based on the sums of LCBD values, wetlands contributed 20.54% to the total variance-based β-diversity, croplands 20.15%, grasslands 20.04%, shrublands 19.69%, and forests 19.57% (Fig. 2b). The total γ-diversity comprised 1140 species. The plant γ-diversity within each ecosystem was 332 species in croplands, 349 in forests, 597 in grasslands, 430 in shrublands, and 177 in wetlands (Fig. 2c).

Fifty-five species were non-native, including 16 archaeophytes and 39 neophytes, and were classified at the national scale as 40 invasive, 14 naturalized, and 1 casual species (Portal to the Flora of Italy, 2025). Seven species were endemic: *Anthemis cupaniana*, *Carex microcarpa*, *Dipsacus ferox*, *Erysimum pseudorhaeticum*, *Euphorbia ceratocarpa*, *Polygala flavescens*, and *Stachys italica*. Eighteen species were red-listed, most of which were associated with wetlands: four are classified as "Endangered" (*Baldellia ranunculoides*, *Hippuris vulgaris*, *Hottonia palustris*, and *Sagittaria sagittifolia*), four as "Vulnerable" (*Butomus umbellatus*, *Leucojum aestivum*, *Ophrys pallida*, and *Ranunculus ophioglossifolius*), and ten as "Near Threatened" (*Carex microcarpa*, *Chamaerops humilis*, *Glyceria spicata*, *Oenanthe fistulosa*, *Osmunda regalis*, *Ruppia spiralis*, *Salix atrocinerea*, *Thymbra capitata*, *Utricularia australis*, and *Zannichellia palustris*). The most species-rich families were Poaceae (136 species), Asteraceae (134), Fabaceae (131), Lamiaceae (47), and Apiaceae (41). The most species-rich genera were *Carex* and *Trifolium* (25 species each), followed by *Vicia* (17), *Medicago* (16), *Ranunculus*, *Festuca*, and *Lathyrus* (15).

Grasslands showed the highest species richness (mean = 20.9, SD = 6.9), whereas wetlands had the lowest (mean = 4.1, SD = 4.8) (Fig. 3a). In contrast, wetlands exhibited the highest mean contribution to β-diversity (mean LCBD = 0.004375, SD = 0.000110). The lowest mean contributions were recorded for forests (mean LCBD = 0.004260, SD = 0.000120) and shrublands (mean LCBD = 0.004256, SD = 0.000141) (Fig. 3b).

Table 1
Results of the Scheirer–Ray–Hare tests assessing the effects of ecosystem type and study site on species richness, LCBD, the number and percentage of unique species, the number and percentage of red-listed species, and the number and percentage of non-native species; Df = degrees of freedom; SS = sums of squares; H = test statistic.

Source of variation	Response				
		Richness		**N° of red list species**	
	df	SS	H	SS	H
Ecosystem	4	468,794	106.009***	24,447	7.653 n.s.
Study site	45	168,100	38.013 n.s.	182,997	57.289 n.s.
Residuals	180	375,788		524,049	
		LCBD		**% of red list species**	
	df	SS	H	SS	H
Ecosystem	4	279,107	63.039***	25,615	7.774 n.s.
Study site	45	229,018	51.726 n.s.	177,983	54.020 n.s.
Residuals	180	505,770		550,904	
		N° of unique species		**N° of non-native species**	
	df	SS	H	SS	H
Ecosystem	4	189,294	43.534***	142,106	42.685***
Study site	45	212,204	48.803 n.s.	258,281	77.581**
Residuals	180	594,227		361,991	
		% of unique species		**% of non-native species**	
	df	SS	H	SS	H
Ecosystem	4	233,177	52.790***	119,422	35.276***
Study site	45	217,043	49.137 n.s.	297,888	87.993***
Residuals	180	561,297		357,940	

n.s. = not significant.
*** $p < 0.001$.
** $p < 0.01$.

Wetlands also had the greatest number of plots with significant LCBD values (21), followed by shrublands (5), croplands (4), and grasslands (1). All 31 plots with significant LCBD values were characterized by rare species, occurring with frequencies of 1–3 across the 230 plots of the dataset. Most of these plots corresponded to vegetation types of high conservation value, including (1) wetlands with *Hottonia palustris*, *Nymphaea alba*, *Potamogeton* spp., *Ruppia* spp., and *Utricularia australis*; (2) shrublands with *Buxus sempervirens*, *Juniperus* spp., *Prunus mahaleb*, and *Salix purpurea*; and (3) the most species-rich plot in the dataset (69 species), a grassland with *Carex montana*, *Festuca alpestris*, and *Bromopsis condensata*. Conversely, cropland plots with significant LCBD values were dominated by noxious agricultural weeds, some of which are non-native invasive species in Italy, including *Ambrosia artemisiifolia*, *Cyperus esculentus*, *Lolium rigidum*, *Portulaca oleracea*, and *Sorghum halepense*.

The highest SCBD values were associated with common species related to wetlands, such as *Phragmites australis*, *Myriophyllum spicatum*, and *Lemna minor*, and to shrublands and forests, such as *Prunus spinosa*, *Rubus ulmifolius*, and *Quercus* spp. (Table 2).

3.3. Unique, red-listed, and non-native species

Grasslands contained the highest total number of unique species (253), followed by forests (117), croplands (107), shrublands (105), and wetlands (80). Only grasslands showed a significantly higher mean number of unique species per plot (Fig. 4a). Wetlands exhibited the highest mean percentage of unique species per plot, followed by grasslands, forests, croplands, and shrublands (Fig. 4b). Wetlands also showed the highest mean number and percentage of red-listed species,

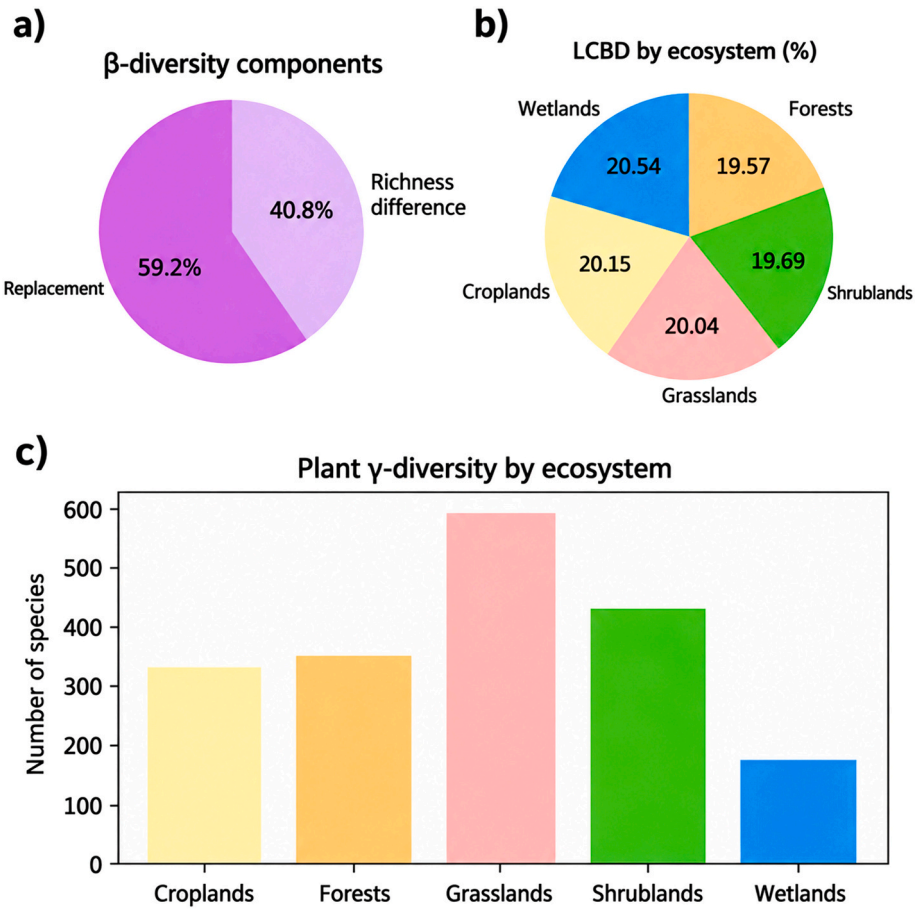

Fig. 2. - (a) percentage contribution of replacement and richness difference to total dissimilarity-based β-diversity; (b) pie chart showing the percentage contribution of the plant communities of each ecosystem type to total variance-based β-diversity, calculated by summing the LCBD values of all plots within each ecosystem type multiplied by 100; (c) total plant γ-diversity for each ecosystem type.

although these differences were not statistically significant (Fig. 4c,d). Croplands and grasslands had a higher number and percentage of non-native species, although numbers remained low (Fig. 4e,f).

3.4. Differences in species composition

We found significant differences in species composition between the plant communities developing in different ecosystems (Table 3). All the post-hoc pairwise comparisons were significant, meaning that each community type was different from all the others.

The NMDS plot (Fig. 5) suggests a compositional gradient consistent with increasing disturbance, primarily along the first ordination axis, and a secondary gradient consistent with decreasing soil moisture, mainly along the second axis, as inferred from the ecology of the associated plant species. The soil moisture gradient was clearly detectable even within non-wetland ecosystem types. Croplands ranged from moist fields (*Lolium multiflorum*, *Sinapis arvensis*) to dry fields (*Euphorbia falcata*, *Silene gallica*). Forests ranged from riparian woods dominated by *Alnus glutinosa* to xeric evergreen oak woods. Shrublands ranged from meso-hygrophilous communities with *Frangula alnus* to xeric evergreen maquis (*Asparagus acutifolius*, *Olea europaea*). Grasslands ranged from mesic meadows (*Poa pratensis, Trifolium repens*) to xeric communities (*Convolvulus cantabrica, Macrobriza maxima*).

4. Discussion

Our analyses quantified the conservation priority of different plant communities in Italian agricultural landscapes, highlighting the key role of farmland wetlands in sustaining vascular plant diversity. Overall, wetlands emerged as the highest conservation priority because they combined the greatest contribution to β-diversity with the highest proportion of unique species and higher values for red-listed species. Grasslands contributed most to total plant diversity and hosted the highest number of unique species, whereas forests, shrublands, and croplands provided complementary contributions by supporting distinct plant communities. The investigated sites exhibited remarkably high plant diversity, confirming the conservation value of agricultural landscapes. Such biodiversity appeared to be associated with the diversity of land uses and management types, as well as with environmental gradients, particularly soil moisture. In this study, we assessed these patterns for the first time at the national scale. Consistent with well-established patterns, grasslands exhibited the highest species richness. Semi-natural temperate grasslands include the highest vascular plant species richness values recorded worldwide at small spatial grains (1 mm^2 to 49 m^2 - Wilson et al., 2012). In agricultural landscapes, the conservation of such local plant species richness is threatened by nitrogen deposition resulting from atmospheric pollution and fertilization, which enhance productivity and acidify soils (Stevens et al., 2010; Socher et al., 2012). Secondary succession driven by land-use changes, particularly the reduction of grazing, further threatens the persistence of these species-rich ecosystems in Europe (Maccherini and Santi, 2012; Wieczorkowski and Lehmann, 2022; Gómez-García et al., 2023). Conversely, wetland plant communities were the poorest in species, as widely shown before (Landucci et al., 2015; Cannucci et al., 2025). Environmental stresses such as prolonged flooding select for a limited number of tolerant species, resulting in species-poor communities

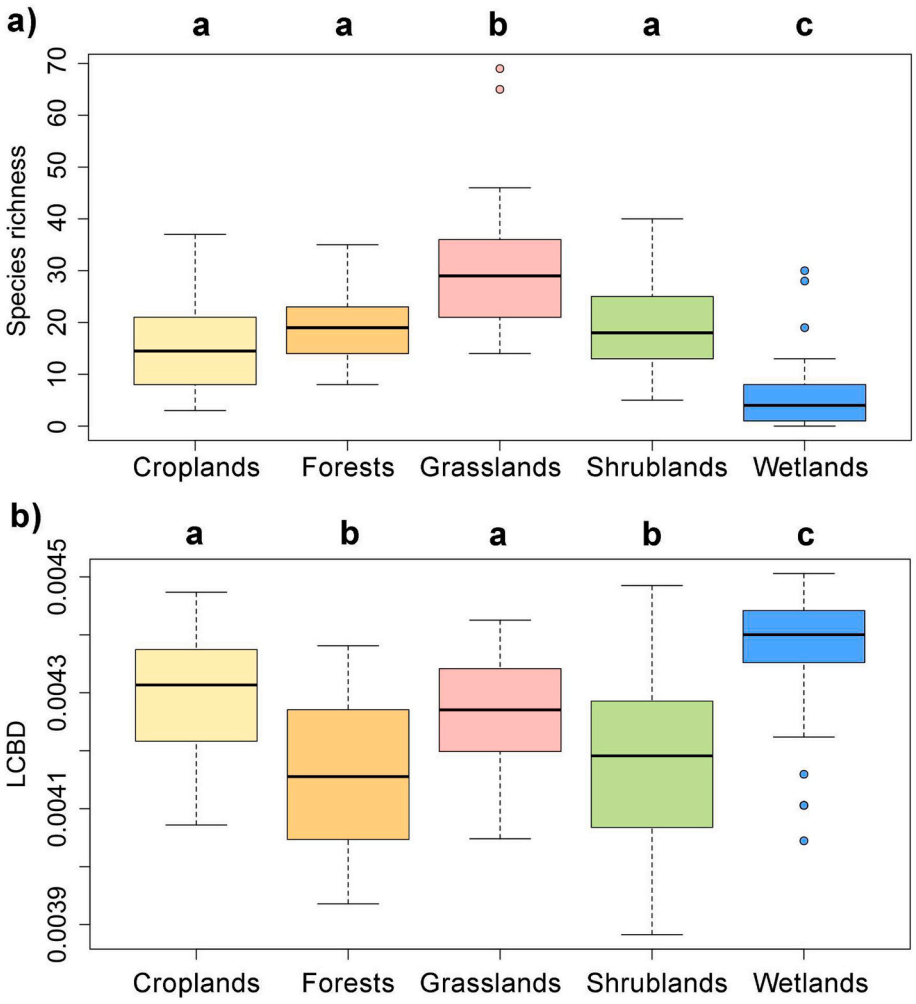

Fig. 3. - Boxplots showing (a) species richness and (b) Local Contribution to Beta Diversity (LCBD) for plant communities across the five ecosystem types. Different letters indicate statistically significant differences based on Dunn's tests with Holm adjustment for multiple comparisons.

Table 2
The ten species with the highest contribution to β-diversity (SCBD) in the dataset.

Species	SCBD	Species	SCBD
Phragmites australis	0.024211	*Quercus ilex*	0.015001
Quercus pubescens	0.022306	*Lemna minor*	0.014356
Prunus spinosa	0.022424	*Quercus cerris*	0.013741
Rubus ulmifolius	0.022131	*Lolium multiflorum*	0.012182
Myriophyllum spicatum	0.016512	*Pistacia lentiscus*	0.012057

dominated by stress-tolerant plants (Grime, 2006). This pattern is particularly evident in permanently inundated sites, so that plant species richness in wetlands decreases with increasing soil moisture (Gaberščik et al., 2018).

Wetlands contributed disproportionately to β-diversity despite their low species richness. Similar patterns have been reported for plant and fish communities across various environmental settings, where species-poor habitats contributed most to β-diversity due to their high species uniqueness (Harper et al., 2022; Fanfarillo et al., 2023b; Pafumi et al., 2024). Croplands also showed a high contribution to β-diversity, although they supported much higher species richness. In extreme ecosystems such as croplands and wetlands, which are shaped by strong anthropogenic or environmental filters, plant species are selected for adaptations to specific environmental pressures. Consequently, the composition of plant communities in these habitats is highly unique, as previously observed across diverse ecosystems including badlands, croplands, coastal dunes, and wetlands (Dubois et al., 2020; Fanfarillo et al., 2023b, 2024b; Pafumi et al., 2024). However, the relationship between abiotic and biotic uniqueness can be context-dependent and sometimes weak (Heino et al., 2022; Snåre et al., 2024). Grasslands and croplands exhibited intermediate LCBD values since they commonly share many generalist species, such as *Cichorium intybus*, *Convolvulus arvensis*, and *Cynodon dactylon* (Chytrý et al., 2024). The low LCBD values observed in forests and shrublands may reflect their species overlap, as many shrub and mantle species often occur in closed forests (e.g., *Cornus mas*, *Crataegus monogyna*, *Ligustrum vulgare*), while several tree species are also found in shrublands (Blasi et al., 2010). Moreover, tree and shrub seedlings and juveniles frequently colonize adjacent ecosystems, particularly within agricultural mosaics that include diverse vegetation types and successional stages (Fanfarillo et al., 2019b; Gómez-García et al., 2023).

Based on floristic composition, the plots with the highest conservation value were mostly wetlands, often characterized by species-poor plant communities harbouring red-listed or rare aquatic species like *Oenanthe fistulosa, Ruppia* spp., *Spirodela polyrhiza, Utricularia australis,* and *Zannichellia palustris*, but also ecologically important vegetation types like shrublands with *Juniperus* spp. and *Buxus sempervirens*. Such elements represent conservation priorities in agricultural landscapes due to their importance as refugia for biodiversity and for their ecological functions (Thiere et al., 2009; Hefting et al., 2013; Valeri et al., 2025). Conversely, the plots with the lowest conservation value

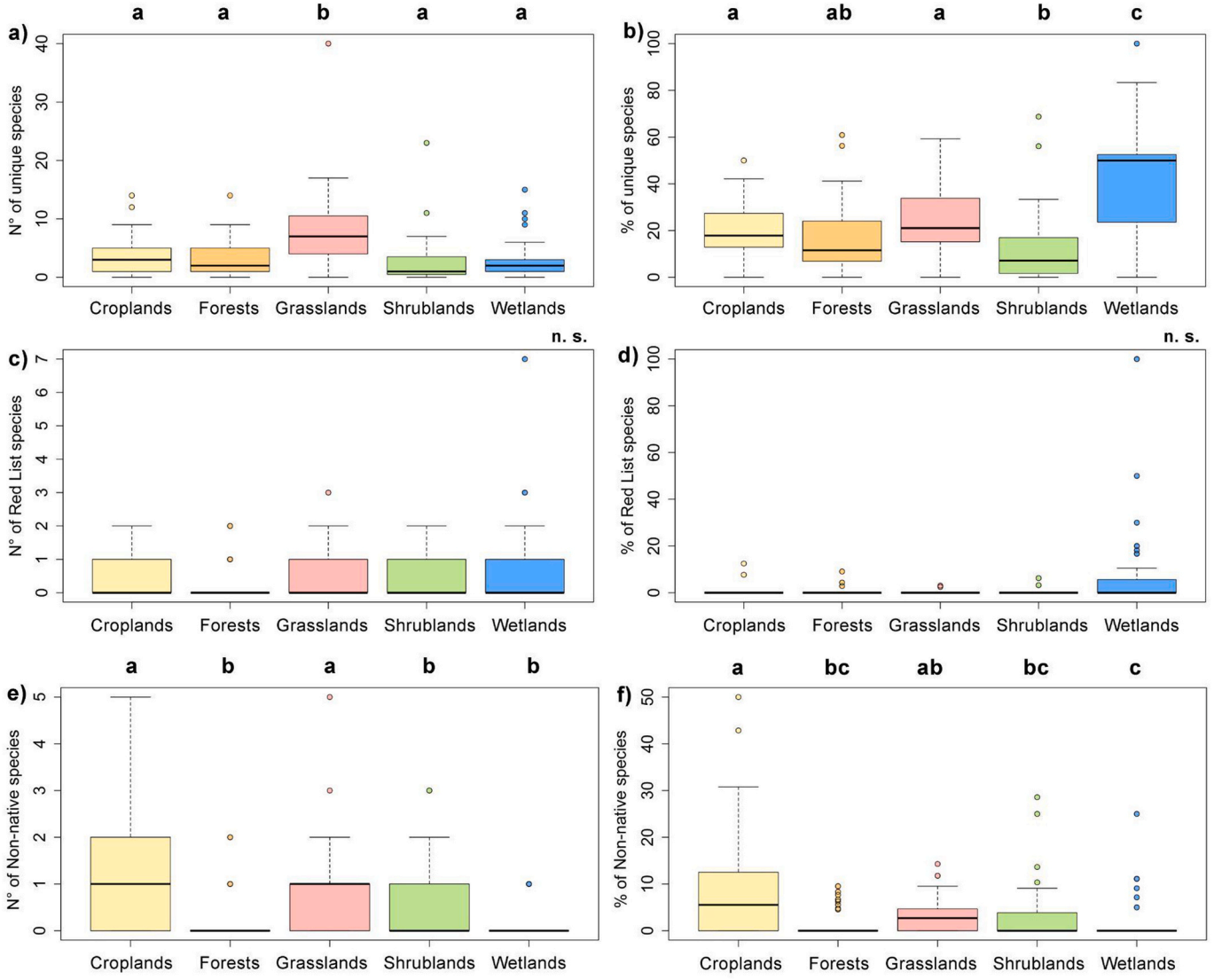

Fig. 4. - Boxplots showing (a) number of unique species, (b) percentage of unique species, (c) number of Red List species, (d) percentage of Red List species, (e) number of non-native species, and (f) percentage of non-native species for plant communities across the five ecosystem types. Different letters indicate statistically significant differences based on Dunn's tests with Holm adjustment for multiple comparisons; n.s. = not significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
PERMANOVA results showing the effect of Ecosystem (fixed factor) and Study site (random factor) on plant community composition; Df = degrees of freedom; SS = sums of squares; MS = mean squares; Pseudo-*F* = pseudo-*F* statistic.

Source of variation	df	SS	MS	Pseudo-*F*
Ecosystem	4	102,720	25,679	7.2661***
Study site	45	224,350	4,985	1.4107***
Residuals	180	636,130	3,534	
Total	229	963,190		

*** $p < 0.001$.

were all croplands, characterized by the presence of some of the most noxious agricultural weeds worldwide, such as *Ambrosia artemisiifolia* and *Sorghum halepense* (Holm et al., 1977; Fanfarillo et al., 2022). Many of these species (*A. artemisiifolia*, *Lolium rigidum*, *Poa annua*, *S. halepense*) have developed glyphosate resistance, and their occurrence can be considered an indicator of intensive agricultural practices and environmental degradation (Hyvönen and Huusela-Veistola, 2008; Heap, 2014).

The highest SCBD values were associated with the species characterizing each of the different ecosystems, i.e., the most frequent and abundant, as previously reported for croplands and coastal dunes (Fanfarillo et al., 2023b; Pafumi et al., 2024). Notably, many species contributing most to β-diversity were associated with wetlands (Chytrý et al., 2024), the ecosystem type that showed the greatest contribution to total β-diversity. Comparable results were observed for fish communities in a tropical seascape and plant communities in coastal dunes, where the species with the highest SCBD values were linked to species-poor habitats, which also had the highest LCBD values (Harper et al., 2022; Pafumi et al., 2024). Woody species associated with shrublands and forests also exhibited high SCBD values in our results. These species characterize the structure of shrub and forest vegetation, which contribute to the diversification of agricultural landscapes, where semi-natural ecosystems are often underrepresented, particularly in intensively farmed areas (Stoate et al., 2009). Moreover, they are linked to structural elements such as woody hedges and field margins, whose role in maintaining biodiversity is well recognized (Billeter et al., 2008). *Quercus* spp. are dominant components of many Italian forest types and characterize forest habitats of high conservation value (Angiolini et al.,

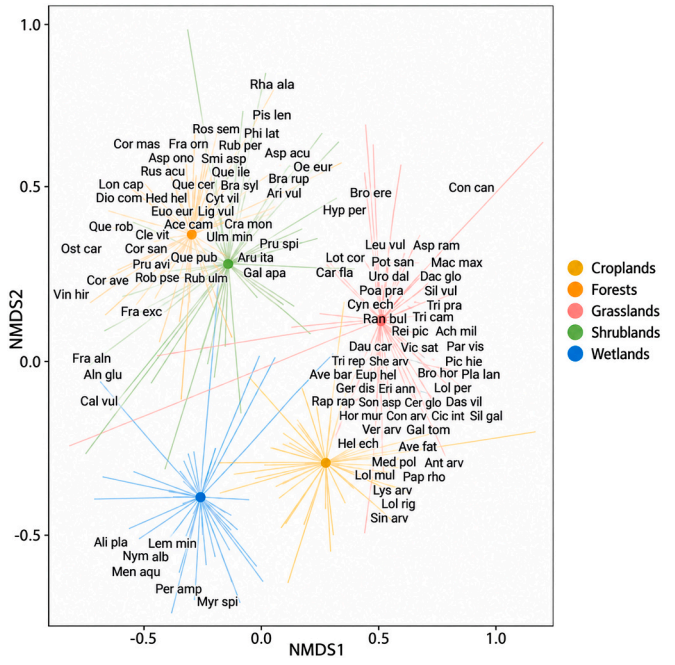

Fig. 5. - Non-metric Multidimensional Scaling Analysis showing the ordination of plant communities by ecosystem type; stress = 0.29. Groups are highlighted as spiderplots. Dots represent group centroids. Grey lines highlight species positions in the ordination space to avoid label overlapping. Full species names are provided in Appendix A.

2021; Selvi et al., 2023). Wetland specialists such as *Phragmites australis*, *Myriophyllum spicatum*, and *Lemna minor* shape reed bed, rooted, and floating aquatic plant communities (Blasi et al., 2010). This evidence highlights that including forest patches, hedges, helophyte-dominated strips and permanently inundated sites in the landscape mosaic is important for maximizing farmland plant diversity.

The proportion of unique species confirmed the importance of wetlands as conservation hotspots; however, grasslands contained the highest absolute number of unique species, consistent with the breadth of their species pool. Semi-natural dry grasslands, in particular, are considered of high conservation value in Europe because they host a large proportion of the continent's plant species and are declining in extent due to reduced grazing pressure and shrub encroachment (Maccherini and Santi, 2012; Wieczorkowski and Lehmann, 2022; Gómez-García et al., 2023). They also include many habitats listed in Annex I of the Habitats Directive (European Commission, 1992). No significant differences in the number or percentage of red-listed species were observed among plant communities from different ecosystems, although wetlands showed higher values for both metrics. This pattern may be explained by the fact that wetland ecosystems are among the most affected by human activities, particularly within agricultural landscapes (van Dam et al., 2025). Due to their vulnerability, wetland plant species were among the most frequently assessed for red-listing purposes in Italy (Orsenigo et al., 2021; Fois et al., 2026). Non-native species were most abundant in croplands and progressively less frequent in grasslands, shrublands, forests, and wetlands, both in terms of species richness and relative proportion. This pattern is consistent with decreasing levels of human disturbance and with previous local-scale evidence (Jauni and Hyvönen, 2010). However, overall invasion levels remained low (mean percentage of non-native species per plot = 3.74%). Although this may suggest a generally good conservation status of the investigated agricultural landscapes, invasion processes may require long time periods to fully develop, and high levels of invasion debt may be present in the meantime (Essl et al., 2011).

The plant communities of all ecosystem types differed significantly in species composition, highlighting their distinctiveness. This provides quantitative evidence of the importance of preserving ecosystem heterogeneity in agricultural landscapes to maximize plant diversity (Strohbach et al., 2015; Bagella et al., 2016; Maskell et al., 2019). Maintaining spatial and temporal diversity among communities of vascular plants and other taxa enhances landscape multifunctionality (Mori et al., 2018). This is particularly relevant in agricultural contexts, where landscape simplification and land-use intensification reduce biodiversity and its associated functions (Benton et al., 2003; Tscharntke et al., 2005; Anderle et al., 2023). From this perspective, intermediate levels of land-use intensity are most effective in promoting heterogeneous landscapes that characterize HNVFs (Strohbach et al., 2015).

The two main gradients of species composition could be interpreted as related to management intensity and soil moisture. Plant communities in agricultural landscapes are often strongly shaped by local management, as already shown in arable fields (Fanfarillo et al., 2023b). Moisture is one of the main factors influencing plant life and shaping local species pools (Whittaker, 1975), while management practices affect species composition through variations in disturbance intensity (Grime, 1973; Bignal and McCracken, 2000). Disturbance, depending on its frequency and magnitude, regulates competitive interactions and thereby influences local diversity (Tilman, 1988). Environmental gradients also play an important role, even in plant communities strongly shaped by farming practices, such as those in croplands (Lososová et al., 2004; Fried et al., 2008; Fanfarillo et al., 2020). Such evidence suggests that preserving both management and environmental gradients is crucial for sustaining high levels of plant diversity in agricultural landscapes. In particular, wetland reclamation for agricultural purposes may greatly impact farmland plant diversity, both due to habitat loss for specialist plants and the reduction of the soil moisture gradient (Gaberščik et al., 2018). Moreover, in regions with a millennia-old history of human presence, many plant species of conservation concern depend on human management to maintain their habitats, which are often of secondary origin (Orsenigo et al., 2018).

We demonstrated that effective plant conservation strategies in farmlands should aim to preserve and enhance the coexistence of multiple ecosystem types. To maximize vascular plant diversity and maintain its ecological functions, it is importanto to maintain diversified agricultural landscapes that integrate ecosystem types spanning a gradient of management and environmental conditions into a complementary, spatially connected mosaic. This recommendation is also consistent with the objectives of the European Nature Restoration Regulation, which promotes increasing the extent of high-diversity landscape features in agricultural ecosystems (European Union, 2024). In particular, introducing, retaining, and restoring wetlands and woody vegetation in such mosaics supports the conservation of associated plant diversity and enhances environmental heterogeneity.

CRediT authorship contribution statement

Emanuele Fanfarillo: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Giovanni Bacaro:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Gianluigi Bacchetta:** Writing – review & editing, Investigation, Data curation. **Simonetta Bagella:** Writing – review & editing, Investigation, Data curation. **Elena Barni:** Writing – review & editing, Investigation, Data curation. **Gianmaria Bonari:** Writing – review & editing, Investigation, Data curation. **Gabriella Buffa:** Writing – review & editing, Investigation, Data curation. **Orazio Caldarella:** Writing – review & editing, Investigation, Data curation. **Giulia Calderisi:** Writing – review & editing, Investigation, Data curation. **Giacomo Cangelmi:** Writing – review & editing, Investigation, Data curation. **Marco Canella:** Writing – review & editing, Investigation, Data curation. **Silvia Cannucci:** Writing – review & editing, Investigation. **Maria Carmela Caria:** Writing – review & editing, Investigation, Data curation. **Miris Castello:**

Writing – review & editing, Investigation, Data curation. **Donatella Cogoni:** Writing – review & editing, Investigation, Data curation. **Gemma Chiaffarelli:** Writing – review & editing, Investigation, Data curation. **Alba Cuena-Lombraña:** Writing – review & editing, Investigation, Data curation. **Martina D'Agostino:** Writing – review & editing, Investigation, Data curation. **Michele Dalle Fratte:** Writing – review & editing, Investigation, Data curation. **Leopoldo de Simone:** Writing – review & editing, Investigation, Data curation. **Silvia Del Vecchio:** Writing – review & editing, Investigation, Data curation. **Thomas Deola:** Writing – review & editing, Investigation, Data curation. **Maria Carla De Francesco:** Writing – review & editing, Investigation, Data curation. **Edy Fantinato:** Writing – review & editing, Investigation, Data curation. **Emmanuele Farris:** Writing – review & editing, Investigation, Data curation. **Giuseppe Fenu:** Writing – review & editing, Investigation, Data curation. **Tiberio Fiaschi:** Writing – review & editing, Investigation, Data curation. **Mauro Fois:** Writing – review & editing, Investigation, Data curation. **Lorenzo Gianguzzi:** Writing – review & editing, Investigation, Data curation. **Lorenzo Lastrucci:** Writing – review & editing, Investigation, Data curation. **Lorenzo Lazzaro:** Writing – review & editing, Investigation, Data curation. **Michele Lonati:** Writing – review & editing, Investigation, Data curation. **Vanessa Lozano:** Writing – review & editing, Investigation, Data curation. **Alfredo Maccioni:** Writing – review & editing, Investigation, Data curation. **Andrea Mainetti:** Writing – review & editing, Investigation, Data curation. **Giacomo Marengo:** Writing – review & editing, Investigation, Data curation. **Francesco Mascia:** Writing – review & editing, Investigation, Data curation. **Chiara Minuzzo:** Writing – review & editing, Investigation, Data curation. **Alice Misuri:** Writing – review & editing, Investigation, Data curation. **Michele Mugnai:** Writing – review & editing, Investigation, Data curation. **Luca Murgia:** Writing – review & editing, Investigation, Data curation. **Emilia Pafumi:** Writing – review & editing, Investigation, Data curation. **Glauco Patera:** Writing – review & editing, Investigation, Data curation. **Giovanna Potenza:** Writing – review & editing, Investigation, Data curation. **Leonardo Rosati:** Writing – review & editing, Investigation, Data curation. **Simona Sarmati:** Writing – review & editing, Investigation, Data curation. **Eugenia Siccardi:** Writing – review & editing, Investigation, Data curation. **Angela Stanisci:** Writing – review & editing, Investigation, Data curation. **Gianmarco Tavilla:** Writing – review & editing, Investigation, Data curation. **Maria Teresa Tiloca:** Writing – review & editing, Investigation, Data curation. **Valeria Tomaselli:** Writing – review & editing, Investigation, Data curation. **Ilda Vagge:** Writing – review & editing, Investigation, Data curation. **Daniele Viciani:** Writing – review & editing, Investigation, Data curation. **Giulio Zangari:** Writing – review & editing, Investigation, Data curation. **Claudia Angiolini:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Simona Maccherini:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Emanuele Fanfarillo reports financial support was provided by European Union. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112087.

Data availability

Data will be made available on request.

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