



Drivers of diversity of arable plant communities in one of their European conservation hotspots

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Abstract

The changes of agriculture led to deep transformations of arable plant diversity. The features of arable plant communities are determined by many anthropic, environmental, and geographic drivers. Understanding the relative importance of such drivers is essential for conservation and restoration purposes. In this work, we assessed the effects of agronomic, climatic, geographic, and landscape features on α -diversity, β -diversity, and composition of winter arable plant communities across continental Italy, a European hotspot of arable plant diversity. Using redundancy analysis and variation partitioning, we observe that the selected groups of variables explained a restrained to moderate proportion of the variation in diversity and composition, depending on the response (5.5–23.5%). We confirm previous evidence that climate and geographic location stand out in determining the features of arable plant communities in the country, followed by the type of rural area. The surrounding landscape has a subordinate influence but affects both α and β -diversity. The α -diversity is higher in traditional agricultural areas and in landscapes rich in woody vegetation, while it is lower in warmer areas. Species composition is determined by climate, latitude, and the type of rural area, but not by landscape. Total β -diversity is mainly explained by climate and latitude, and subordinately by the agricultural context and landscape. Its components are explained by latitude and climate (replacement) and agricultural context and climate (richness difference). The local contribution to β -diversity of single sites suggested a good conservation status of the studied communities. We discuss the implications of our findings in the light of conservation and restoration of vanishing arable plant communities.

Keywords α -diversity · Arable weed · β -diversity · Biodiversity pattern · Landscape ecology · Variation partitioning

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Introduction

Stopping biodiversity loss is one of the main challenges of modern times (Díaz et al. 2019). Agriculture is a major threat to nature conservation, but ancient low-input agricultural systems are also important for biodiversity (Wright et al. 2012). In agricultural landscapes, arable plants are essential for biodiversity conservation and they provide environmental and agronomic services (Marshall et al. 2003; Adeux et al. 2019). Such species are adapted to recurrent tillage, since developing among arable crops (Holzner 1978). Due to the intensification of agriculture, they are declining in many areas, especially in Europe (Storkey et al. 2012; Meyer et al. 2013; Richner et al. 2015; Fanfarillo et al. 2019a). Thus, their preservation is relevant for biodiversity conservation, particularly in the Old World, where they originated or anciently established (Türe and Böcük 2008; Nowak et al. 2014; Albrecht et al. 2016; Janssen et al. 2016; Chytrý et al. 2020). At middle-high latitudes, two broad ecological groups of arable plants are detectable: those having a winter-spring life cycle/phenology and those having a summer-autumn life cycle/phenology, respectively developing in winter and summer crops (Holzner 1978). Many winter arable plants are of conservation concern in Europe, due to their specialization and vulnerability to agricultural intensification (Storkey et al. 2012; Richner et al. 2015). Often, their conservation is totally dependent on the maintenance of low-input cereal cultivation, contrarily to most summer arable plants that colonize many disturbed habitats (Fanfarillo et al. 2020a, 2022). European traditional agricultural areas are hotspots of arable plant diversity, with Italy hosting the best-preserved arable habitats, especially in hills and mountains of the peninsula (Janssen et al. 2016; Fanfarillo et al. 2019b, 2020a, b; Hurford et al. 2020). However, despite several highly specialist arable plants are in the Red List of the Italian flora, arable plant diversity was neglected in the definition of Italian important plant areas (Blasi et al. 2011; Orsenigo et al. 2021).

The determinants of the features of arable plant communities include agronomic, climatic, edaphic, and landscape factors. Among management factors, the current and preceding crop type significantly affect species composition. Climate and geographic location are drivers of major species turnovers as well, especially at broad scales (Fried et al. 2008; Lososová et al. 2004; Šilc et al. 2009; Nowak et al. 2015; Fanfarillo et al. 2020b). Landscape-scale processes affect arable plant communities at the local scale, in the order of hundreds of meters from arable fields (Petit et al. 2011). However, landscape has different and contrasting effects depending on which predictive and response variables are assessed (Gaba et al. 2010; Lüscher et al. 2014; Petit et al. 2016; Metcalfe et al. 2019). Due to the number of different drivers involved, the need to rely on a multifactor approach to explain the variation of arable plant diversity is evident.

Measuring biodiversity is one of the main issues of community ecology. Besides species richness at a given site (α -diversity) and the total species richness of an area (γ -diversity), studying the organization and variation of communities across space and time (β -diversity) is important to understand the processes that generate and maintain biodiversity in ecosystems, with relevant implications for biodiversity conservation (Legendre and De Cáceres 2013; Ruhí et al. 2017). β -diversity is usually measured through dissimilarity indices, thus ranging between 0 and 1. It can be decomposed into replacement (species turnover) and richness difference (species gain and loss). Measuring and interpreting these two components allows understanding the drivers of differentiation between communities across a study area since they can be analyzed using explanatory variables (Legendre 2014). As

regards arable plant communities, patterns of β -diversity vary considerably across years, seasons, regions, landscapes, crops, and types of agricultural management (Lososová et al. 2004; de la Fuente et al. 2006; Armengot et al. 2012; Alignier and Baudry 2016). While several works investigated the patterns of total β -diversity in arable plant communities, its replacement and richness difference components are scarcely studied. Alignier and Baudry (2016) assessed them in field margins at a local scale in France, along a temporal gradient, and showed that changes in β -diversity were dominated by replacement.

Due to its considerable decline, several conservation strategies for arable plant diversity were proposed in Europe. These include “land sharing” options, in which conservation is carried out into the same fields dedicated to crop production, and “land sparing” options, with the creation of fields dedicated to conservation. These conservation measures might both be successful (Haggar et al. 2021). Low-intensity management is effective in sustaining arable plant diversity, as well as land sparing options like conservation headlands, uncropped margins, wildflower strips, and arable reserves (Albrecht et al. 2016; Wietzke et al. 2020). Evidence suggests that arable plant diversity should be preserved at the field scale (Gonthier et al. 2014). Field edges seem to be a good refuge for arable plants, so that the maintenance of favorable conditions on field margins can be a good option for their conservation (Fried et al. 2009). However, typical arable plants can be outcompeted by species from surrounding habitats on field margins (Metcalf et al. 2019). In spite of the concerns by scientists about preserving arable plant diversity, there is still a big regulatory gap for its conservation in EU policies. In the Annex I of the Habitats Directive, no anthropogenic habitat is present, inconsistently with the fact that extensively managed arable land (EUNIS habitat I1.3) is a habitat Red-listed as “Endangered” (Janssen et al. 2016).

Despite not all the arable plants need conservation, preserving rare arable plants alone might not be effective. For instance, there is evidence that some rare arable species share a lot of pollinators with more common species, the latter being the primary target of such pollinators (Gibson et al. 2006). Moreover, rare and threatened arable plants are known to co-occur under favorable conditions (Fanfarillo et al. 2020c). This implies that conservation measures should target whole communities, rather than single species.

Investigating the influence of different sets of variables on biotic communities is crucial to understand community variation across time and space, and to define conservation strategies (Maccherini et al. 2011; Barbato et al. 2019; Giallonardo et al. 2019; Hu et al. 2022). Environmental and geographic features are pivotal for the survival of arable plant species (Walker et al. 2007; Fanfarillo et al. 2020b). Furthermore, species reintroduction might be necessary to restore typical arable plant communities in areas with impoverished seed banks, where they may not spontaneously recover once they have disappeared, even if favorable conditions are established (Hyvönen 2007; Wietzke et al. 2020). Thus, understanding the importance of different factors in determining community features is essential for a correct, site-specific definition of both conservation and restoration strategies.

So far, no study investigated the joint effects of different anthropic and natural groups of factors on arable plant communities in a conservation hotspot. To provide a first, thorough understanding of the patterns of such biodiversity and of their drivers at such scale, in this work we selected four sets of agronomic, climatic, geographic, and landscape variables and investigated their effects on 105 recently surveyed arable plant communities of Italy. We assessed the effects of these sets of variables on α -diversity (species richness), β -diversity

and its components (replacement and richness difference), and species composition, using redundancy analysis and variation partitioning approaches.

Materials and methods

Study area and data collection

The study area stretches for about 1,000 km across mainland Italy (Fig. 1). Bioclimate is either Mediterranean or Temperate. The Mediterranean bioclimate is distinguished by summer drought and it is present along coasts and at lower elevations and latitudes. The Temperate bioclimate is characterized by absent or reduced summer drought, and it is present in the north and in inland and upland areas. Mean annual temperatures range between 10 and 19°C and mean annual precipitations vary between 500 and 2000 mm (Pesaresi et al. 2017). Geological substrates are mainly sedimentary (limestone, flysch, dolomite), with some volcanic and metamorphic areas along the western Peninsula and recent alluvial deposits in lowlands (Bosellini et al. 2017). The most frequent soil types are Cambisols, Luvisols, Regosols, and Phaeozems (Costantini et al. 2013).

Ahead of sampling, we searched for a gradient across Italy representing as much as possible the relevant geographic, environmental, and agricultural diversity of the country. We could detect a proper gradient going from the western part of the Po Plain south-eastwards all along the Italian Peninsula. Our research targeted the arable plant communities of winter-annual crops. Given the impossibility to check a priori for the presence of the target crops and for the accessibility of sites, we haphazardly selected the fields right during the surveys.

In the springs of 2018 and 2019, we carried out a plot-based survey on arable plant communities of winter cereals (*Avena sativa*, *Hordeum vulgare*, *Lolium multiflorum*, *Triticum aestivum*, *T. turgidum* subsp. *durum*), winter or spring legumes (*Cicer arietinum*, *Lathyrus oleraceus*, *Medicago sativa*, *Trifolium alexandrinum*, *T. squarrosum*, *Trigonella foenum-graecum*, *Vicia faba*, *V. sativa*) and winter fodder mixes (cereals, legumes, and cereal-legume mixtures) across mainland Italy. In the study area, such crop types are allied regarding their arable flora, since having all a winter-spring seasonality (Fanfarillo et al. 2020a). We surveyed 149 winter arable fields, regularly distributed across the study area and broadly covering the diversity of agricultural managements and environmental conditions of mainland Italy. We excluded the Alps, where the target crops have minor importance compared to the rest of the country. The surveyed fields are located between 45.0–39.0°N and 7.5–17.0°E, at elevations between 2 and 1,100 m a.s.l. (Fig. 1). In each field, we placed a plot of 1 × 16 m (149 total plots). Each plot was oriented along seed-drill lines and located in the inner part (5–10 m from the edge, depending on field size) to avoid edge effects. The plot size was selected according to Chytrý and Otýpková (2003). The plot shape was selected to maximize the number of recorded species and increase the ease of movement in the field (Güler et al. 2016; Fanfarillo et al. 2020b). In each plot, we recorded all the occurring vascular plant taxa (including crop species) and attributed Braun-Blanquet cover values (Braun-Blanquet 1964). Species were identified according to Pignatti et al. (2017–2019). Taxonomic nomenclature follows Bartolucci et al. (2018) for native species, Galasso et al. (2018) for non-native species, and following updates (Portal to the flora of Italy 2022; avail-

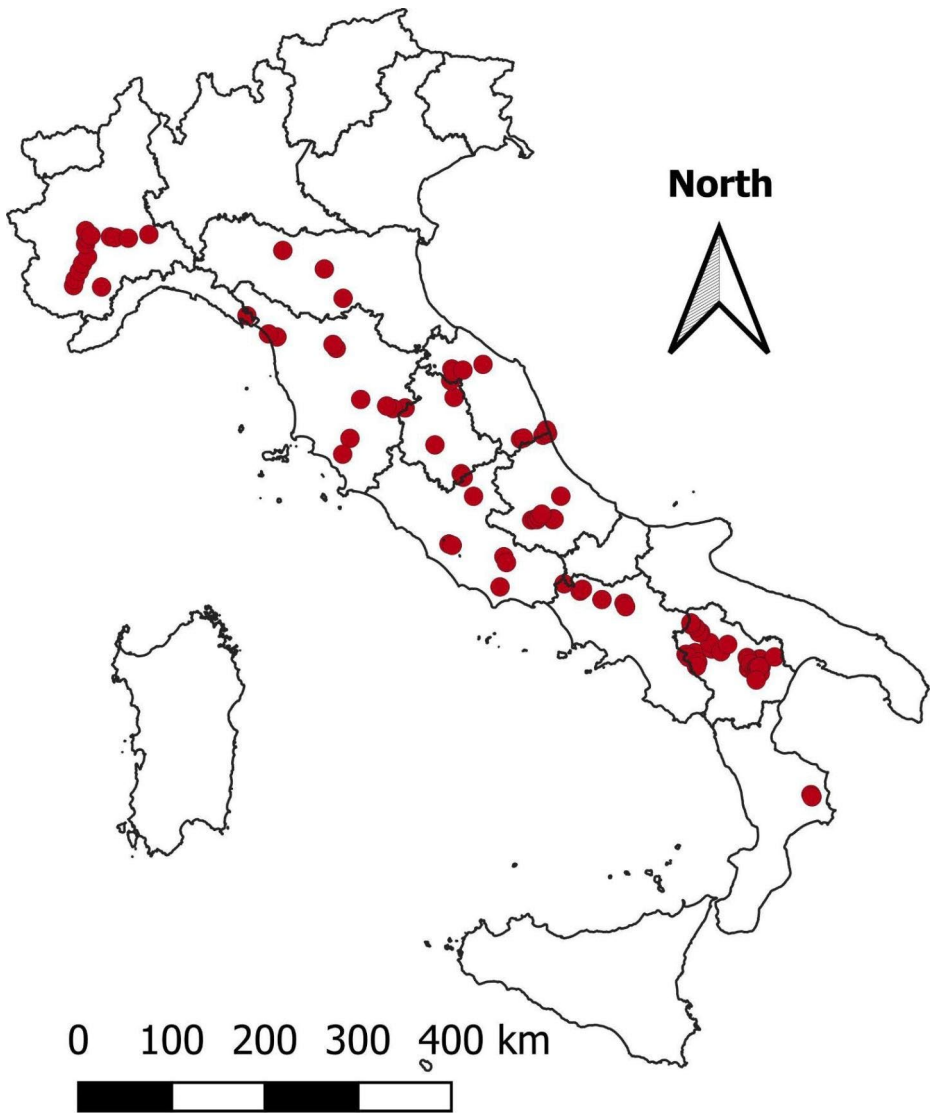


Fig. 1 Distribution of the surveyed fields in Italy (red dots); the black lines are the boundaries of Italian administrative regions

able at <http://dryades.units.it/floritaly/index.php>). European rare/threatened arable plant species are classified according to Storkey et al. (2012).

Since the surrounding landscape influences arable plant communities at the scale of hundreds of meters (Gaba et al. 2010; Petit et al. 2011), we assessed landscape features within a 400 m radius circle around each sampling plot. In case of overlapping between

the buffers, only the first plot in order of sampling was selected. Thus, we selected 105 plots out of 149 (88 winter cereals, 10 forage mixes, 7 legumes). Land use types were identified through photointerpretation from Landsat/Copernicus satellite and Street View (<https://www.google.it/maps>), using the most detailed scale available (1:500), a minimum mapping unit of 10 m², and the most recent images for each site. The landscape components were classified into seven land use categories: (1) water bodies; (2) woods, shrublands, other woody or functionally allied vegetation types (including garrigues and reed beds), and isolated trees and shrubs (hereafter “woody vegetation”); (3) open fields (including arable land, pastures, and meadows); (4) permanent crops (olive groves, fruit orchards, poplar plantations, vineyards, etc.); (5) artificial surfaces; (6) artificial vegetation (gardens, parks); (7) bare rock and natural erosion surfaces (Badlands, gravels, and rocky outcrops) (Fig. 2). After converting the vectorial file in a raster format, the abundance of each land use type (m²) and the Shannon index were calculated as measures of landscape heterogeneity for each buffer, using the QGIS plugin LecoS version 3.0.0 (Jung 2016). All the landscape analyses were carried out in QGIS v. 3.20 (QGIS Development Team 2021; available at <https://www.qgis.org/en/site/>).

Retrieval of explanatory variables

We compiled a dataset including agronomic (amount of fertilizers per province; amount of herbicides per province; type of rural area) (ISTAT 2019; available at <http://dati.istat.it/>; Italian Ministry of Agriculture, Food and Forestry 2010; available at https://www.reterurale.it/downloads/cd/PSN/Psn_21_06_2010.pdf), geographic (latitude; longitude; elevation), climatic (yearly positive temperature, measured in accumulated degree days above 0 °C during the year as a proxy of the growth season; year total precipitation; continentality index - Pesaresi et al. 2017), and landscape factors (abundance of each land use type; field size; landscape Shannon diversity) for each plot. We defined the types of rural areas according

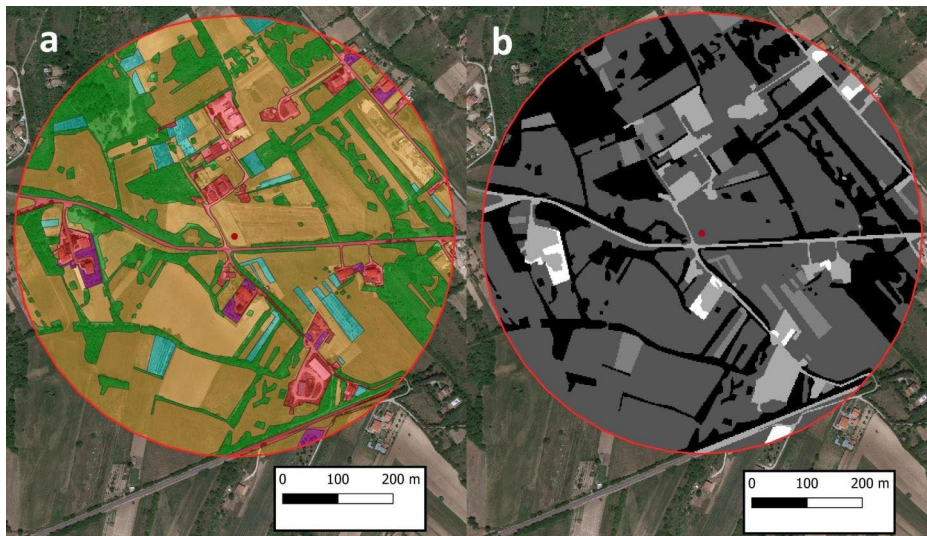


Fig. 2 Example of photointerpretation from satellite images in a 400 m radius buffer around a sampling plot (red dot): (a) vectorial format; (b) raster format

to the National Rural Network classification. These were ordered according to a gradient of increasing agricultural intensification/land use intensity: (1) Rural areas with development problems; (2) Intermediate rural areas; (3) Rural areas with intensive and specialized agriculture; (4) Urban and peri-urban areas.

Selection of explanatory variables

For all the analyses, crop species were removed and species covers were converted into the corresponding percentage values in Turboveg (Hennekens and Schaminée 2001). All the analyses were carried out in R (R Core Team 2021). We selected explanatory variables through a two-step process. After implementing a database with all the potentially useful variables, we checked correlations between them. When two variables were highly correlated ($r \geq -0.7$ and $r \geq 0.7$, Spearman test), we randomly removed one of them. The remaining variables were grouped into agronomic, geographic, climatic, and landscape factors.

Within each of such groups, we further carried out a forward selection procedure of explanatory variables (function “forward.sel” in the package *adespatial*) (Dray et al. 2019). The “forward.sel” function performs a forward selection of predictors by permutation of residuals under a reduced model, for both univariate and multivariate response data. The procedure stops when at least one between the following parameters reaches the established value: (1) maximum variables to be selected (default threshold: number of plots -1); (2) R^2 of the model (default threshold: 0.99); (3) adjusted R^2 of the model (default threshold: 0.99); (4) p-value of a variable (default threshold: $p=0.05$); (5) difference in the R^2 of the model with the previous step (default threshold: 0.001) (Dray et al. 2019). The variables were tested against species richness, species composition (species by site matrix with Hellinger transformation of percentage cover values), total β -diversity, and replacement and richness difference components of β -diversity. β -diversity and its components were calculated through the function “beta.div.comp” in *adespatial*, building three distance matrices (dissimilarity measure: Ruzicka index). The variables selected for at least one analysis are reported in Table 1.

Response variables

To assess the relative contribution of the four groups of variables in explaining the total variation in α -diversity, total β -diversity and its components, and species composition, we used a variance partitioning technique (function “varpart” in the package *vegan* - Oksanen et al. 2021). This method partitions the variation of each response variable (community data as a species by site matrix, or community dissimilarities expressed by total β -diversity and its partition in richness difference and replacement), with respect to two to four explanatory groups. If the response is a single vector (e.g., α -diversity), partitioning is made by partial regression. We tested the significance of the whole models and of the pure effects of the groups of variables through anova tests. The pure effects of the groups of variables were calculated by conditioning the effects of the other groups of variables in partial RDA (pRDA). To visualize the gradients of species composition in relation to the explanatory variables, we used Redundancy Analysis (“rda” function in *vegan*), assessing the significance of the first two axes through permutation tests (function “anova.cca” in the package *vegan*, $n \text{ perm}=999$), and those of single variables through anova tests.

Table 1 Descriptive statistics of the variables used in at least one of the analyses (grouped into agronomic, geographic, climatic, and landscape factors) after the forward selection procedures on α -diversity, species composition, total β -diversity, replacement, and richness difference. SD=Standard deviation; CV=Coefficient of variation

Group of variables	Variable	Mean (min-max)	SD	CV
Agronomic	Rural area type (land use intensity)	1.885 (1–4)	1.01	53.69
Geographic	Latitude (m N, WGS84)	4,671,315 (4,338,068–5,005,098)	187,604	4.02
Climatic	Yearly Positive Temperature (Degree Days)	1,672 (1,182–2,419)	173	10.37
	Year precipitation (mm)	823 (571–1507)	201	24.43
Landscape	Abundance of woody vegetation (m ²)	88,840 (50–323,956)	75,930	85.47
	Abundance of artificial surfaces (m ²)	47,337 (1,060–218,412)	45,093	95.26
	Abundance of water surfaces (m ²)	2,186 (0–50,550)	6,323	2.89
	Field size (ha)	3.04 (0.12–24.52)	4.19	1.38

To assess the local contribution to β -diversity of single plots and single species, we calculated the LCBD (Local Contribution to Beta Diversity – comparative indicators of the ecological uniqueness of the sites) and SCBD (Species Contribution to Beta Diversity – degree of variation of individual species across the study area) values, respectively (Legendre and De Cáceres 2013). We tested the significance of LCBD values by random, independent permutations through the function “beta.div” in *adespatial*.

Results

Patterns of plant diversity

The α -diversity (range 5–35 species) was higher in the hilly and mountainous areas of the peninsula, with several hotspots especially in the south. The same patterns emerged based on rare/threatened species, meaning that species-richer communities were also richer in species of conservation concern (Fig. 3).

The total β -diversity among plant communities was 0.45. The replacement component was the most important (0.39, 85.7%), while the richness difference had a subordinate role (0.06, 14.3%). The γ -diversity (total number of species) was of 314 taxa, the most frequent being *Papaver rhoeas* (77 plots, 73.3%), *Convolvulus arvensis* (57 plots, 54.3%), *Lysimachia arvensis* (54 plots, 51.4%), *Lolium multiflorum* (50 plots, 47.6%), and *Polygonum aviculare* agg. (50 plots, 47.6%). We detected 22 rare/threatened species (0–7 per plot), the most frequent of which were *Legousia speculum-veneris* (38 plots, 36.2%), *Galium tricoratum* (35 plots, 33.3%), *Scandix pecten-veneris* (29 plots, 27.6%), *Ranunculus arvensis* (26 plots, 24.8%), and *Adonis annua* (25 plots, 23.8%). Among the ones ranked as the most threatened in Europe, there were *Agrostemma githago* (5th), *Adonis flammea* (6th), *Adonis aestivalis* (8th), *Scandix pecten-veneris* (9th), and *Lolium temulentum* (10th).

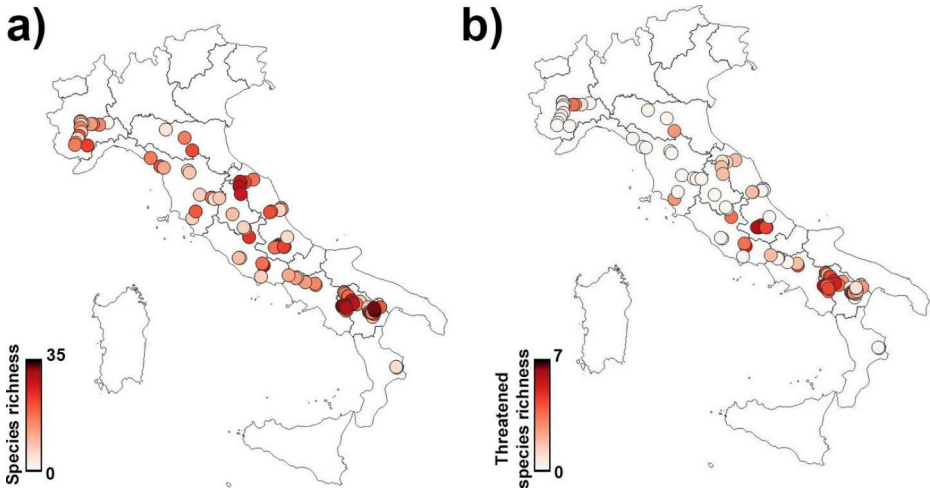


Fig. 3 Total (a) and rare/threatened (b) species richness (α -diversity) across the study area

Drivers of α -diversity, species composition, and β -diversity

Variation partitioning on α -diversity revealed that the selected variables accounted for by 23.5% of the variability in species richness ($p=0.001$). Agronomic factors (rural area type) accounted for by 10.7%, climatic factors (temperature) 5.1%, and landscape factors (abundance of woody vegetation) 4.1% (Fig. 4a). α -diversity values decreased along the agricultural intensification gradient based on the type of rural area (Fig. 5a) and with increasing temperature (Fig. 5b), while they increased with increasing abundance of woody vegetation in the landscape (Fig. 5c).

Variation partitioning on species composition revealed that the selected variables accounted for by 7.5% of the variation ($p=0.001$). The analysis highlighted a significant effect of agronomic factors (rural area type), climate (temperature and precipitation), and latitude. On the contrary, landscape factors (abundance of artificial surfaces and abundance of woody vegetation) had no significant effects (Fig. 4b).

European rare and threatened species were negatively related to the abundance of artificial surfaces and positively related to the abundance of woody vegetation. Generalist taxa like *Lysimachia arvensis* and *Polygonum aviculare* agg. had an opposite trend. All the explanatory variables were statistically significant, except for the abundance of woody vegetation (Fig. 6).

The selected variables accounted for by 7.4% of the total β -diversity ($p=0.001$), 5.5% of replacement ($p=0.001$), and 11.6% of richness difference ($p=0.001$). The 1.4% of total β -diversity was explained by latitude, 1.3% by climate (temperature and precipitation), 0.8% by landscape (field size, abundance of artificial surfaces, and abundance of water surfaces), and 0.5% by agronomic factors (rural area type) (Fig. 7a). The 1.8% of the replacement component was explained by latitude and 1% by climate (temperature and precipitation) (Fig. 7b). The 11.4% of the richness difference component was explained by agronomic factors (rural area type) and 4.1% by climate (temperature) (Fig. 7c).

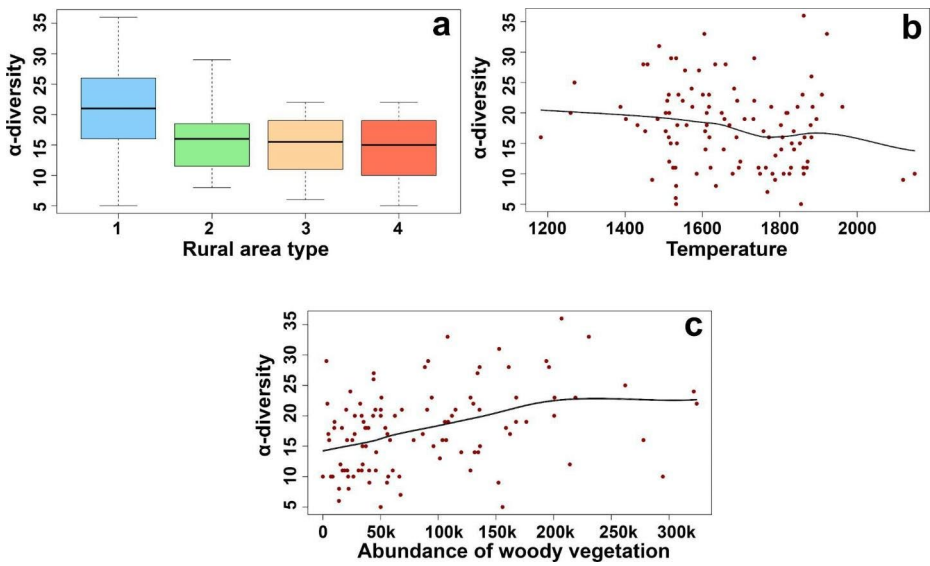


Fig. 5 Patterns of α -diversity (species richness) in the surveyed communities in relation to (a) rural area type (ordered according to increasing agricultural intensity), (b) temperature (Degree Days), and (c) abundance of woody vegetation in the landscape (m^2). Smooth lines are fitted to the data to show the relationships between variables.

The highest contribution to β -diversity across the study area was given by the plots with lower α -diversity (LCBD vs. species richness: Pearson's $\text{cor} = -0.28$, $p < 0.01$), which were also poorer in rare/threatened species (LCBD vs. rare/threatened species richness: Pearson's $\text{cor} = -0.27$, $p < 0.01$). Occasionally, high LCBD values resulted in plots located in ecologically peculiar areas like the Badlands of south-eastern Italy, wetlands, or high elevations (Fig. 8a, b).

The highest contribution to β -diversity was mostly given by the species with high frequencies (SCBD vs. species % frequency: Pearson's $\text{cor} = 0.79$, $p < 0.001$) (Table 2). These included both common and generalist taxa (*Lolium multiflorum*, *Papaver rhoeas*, *Polygonum aviculare* agg.) and species of conservation interest (*Galium tricornerutum*, *Ranunculus arvensis*, *Scandix pecten-veneris*).

Discussion

Our study highlighted novel patterns adding key knowledge on the determinants of arable plant communities. All the tested groups of variables were significant in explaining different aspects of biodiversity, especially latitude, climate, and agronomic factors. This confirms the successfulness of multifactor approaches to understand the organization of life. We observed how different components of diversity are explained to different extents by different sets of variables. The analysis of β -diversity and its components allowed a better comprehension of biodiversity patterns at the community level, improving the baselines for conservation and management planning (Carlos-Júnior et al. 2019). LCBD values were particularly effective in detecting sites with high and low conservation value, synthesizing

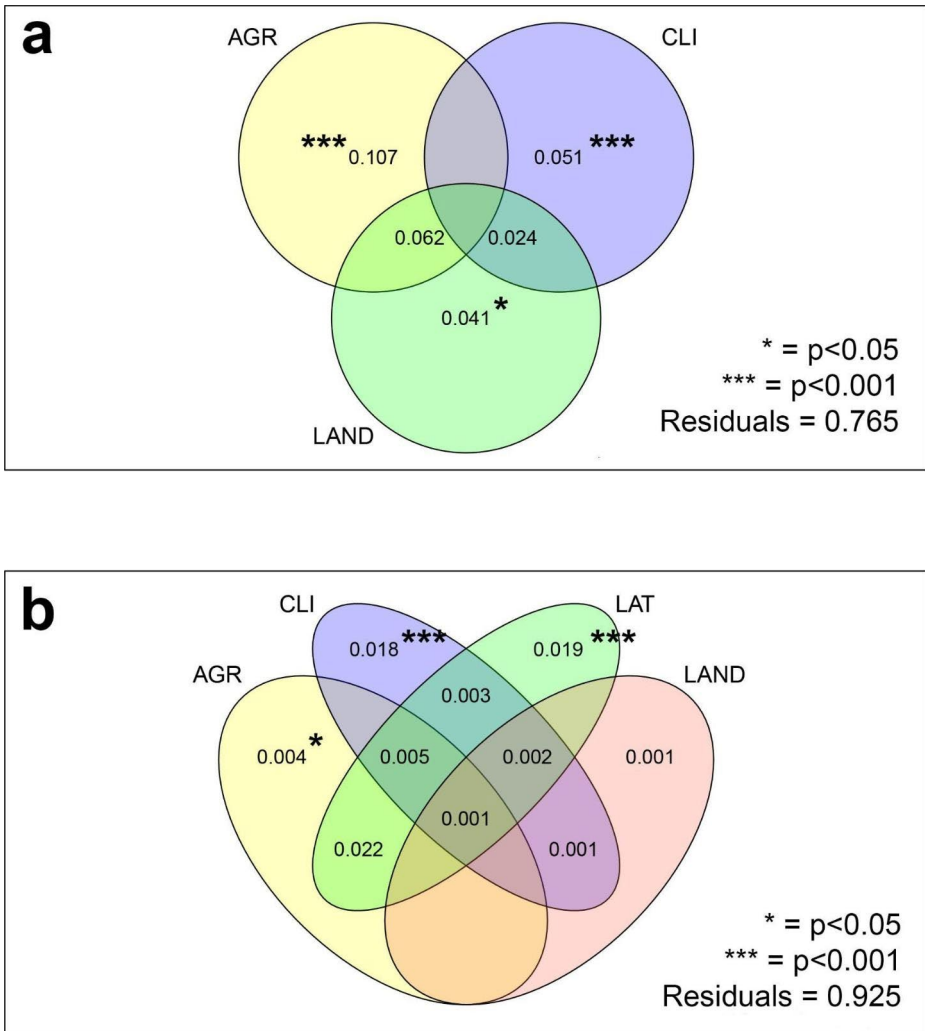


Fig. 4 Venn diagrams showing the relative contributions of the selected groups of variables to the total variation in α -diversity (a) and species composition (b) among plots. AGR=agronomic factors; CLI=climatic factors; LAT=latitude; LAND=landscape factors

the spatial patterns of diversity into one metric that expresses the uniqueness in species composition of single communities (Legendre 2014). Thus, we confirm the usefulness of LCBd values for conservation purposes, as previously highlighted (Hill et al. 2021).

Consistently with previous evidence, the proportion of explained variation on the response variables was relatively restrained. In fact, arable plant communities are among the most human-influenced, and all the attempts to explain their variability resulted in limited success (Lososová et al. 2004; Šilc et al. 2009). The importance of agronomic factors in affecting arable plant diversity was recurrently evidenced in our results, especially as regards the levels of α -diversity and the richness difference component of β -diversity. This

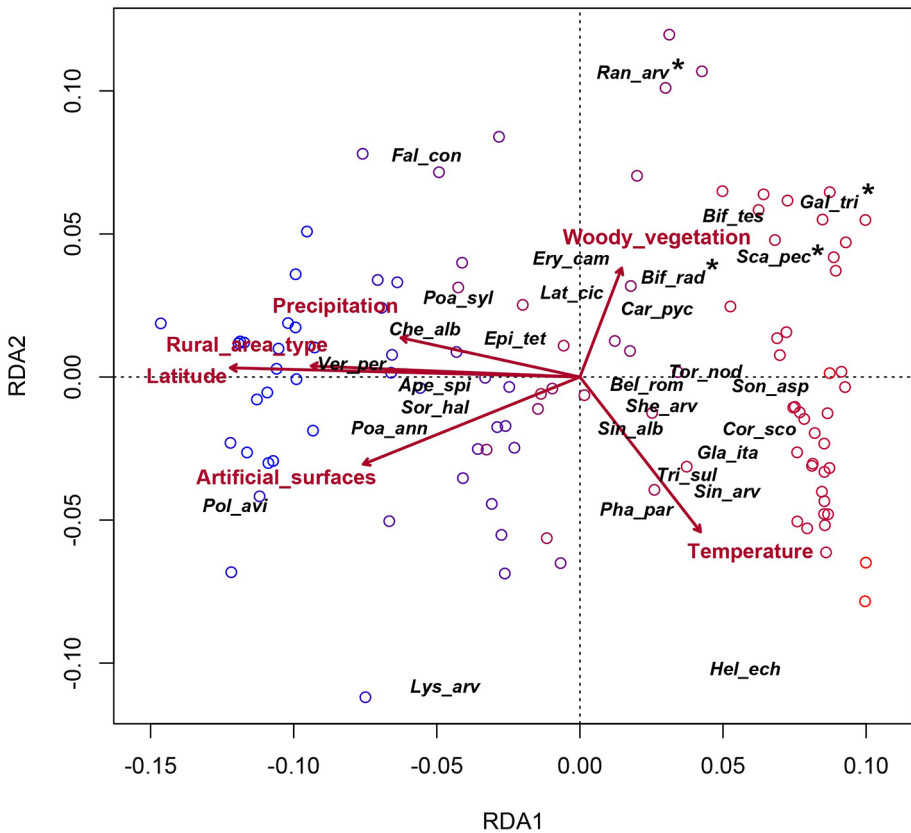


Fig. 6 RDA plot on species composition. Explained variance: RDA1=5.2% ($p=0.001$); RDA2=1.6% ($p=0.001$). Circles represent plots, colored according to the latitudinal gradient (red=south, blue=north). Plotted species have a goodness of fit in the analysis higher than 0.1. Species of European conservation interest according to Storkey et al. (2012) are marked with an asterisk. Ape_spi=*Apera spica-venti*; Bel_rom=*Bellevalia romana*; Bif_rad=*Bifora radians*; Bif_tes=*Bifora testiculata*; Car_pyc=*Carduus pycnocephalus*; Che_alb=*Chenopodium album*; Cor_sco=*Coronilla scorpioides*; Epi_tet=*Epilobium tetragonum*; Ery_cam=*Eryngium campestre*; Fal_con=*Fallopia convolvulus*; Gal_tri=*Galium tricornerum*; Gla_ita=*Gladiolus italicus*; Hel_ech=*Helminthotheca echioides*; Lat_cic=*Lathyrus cicera*; Lys_arv=*Lysimachia arvensis*; Pha_par=*Phalaris paradoxa*; Poa_ann=*Poa annua*; Poa_syl=*Poa sylvicola*; Pol_avi=*Polygonum aviculare* agg.; Ran_arv=*Ranunculus arvensis*; Sca_pec=*Scandix pecten-veneris*; She_arv=*Sherardia arvensis*; Sin_alb=*Sinapis alba*; Sin_arv=*Sinapis arvensis*; Son_asp=*Sonchus asper*; Sor_hal=*Sorghum halepense*; Tor_nod=*Torilis nodosa*; Tri_sul=*Trigonella sulcata*; Ver_per=*Veronica persica*

confirms the relevance of local filtering in affecting the studied communities and suggests that local management is a key factor for their conservation (Bourgeois et al. 2020).

Drivers of α -diversity, species composition, and β -diversity

Consistently with our results, a review of several studies showed that α -diversity of arable plant communities is impacted by local management, but not by landscape complexity (Gonthier et al. 2014). In France, the increasing proportion of organic fields in the surround-

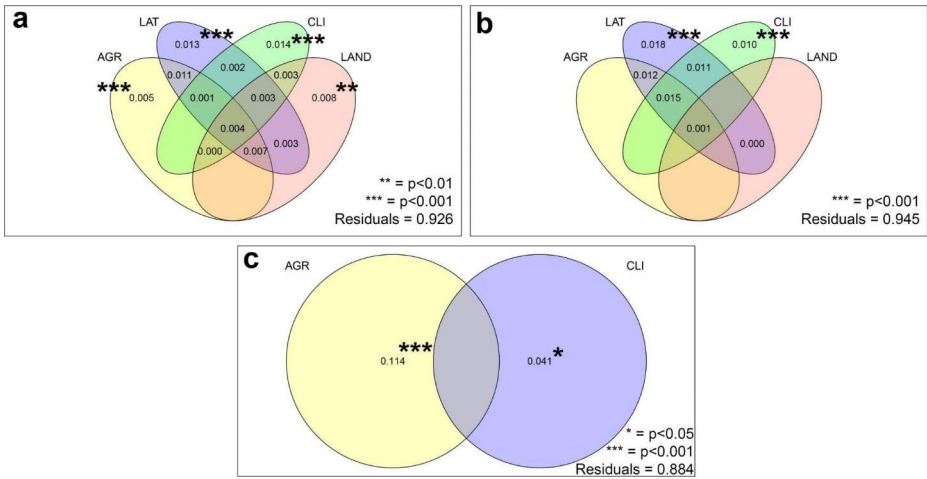


Fig. 7 Venn diagrams showing the pure and shared contributions of the selected groups of variables to the variation in the total β -diversity (a), replacement (b), and richness difference (c) among plots. AGR = agronomic factors; CLI = climatic factors; LAT = latitude; LAND = landscape factors

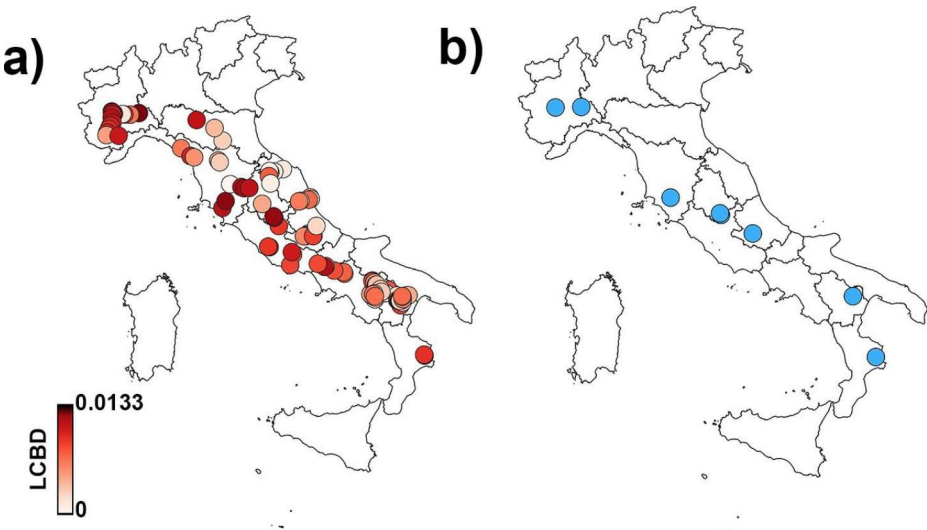


Fig. 8 (a) Local Contribution to Beta Diversity (LCBD) values (min=0.0065, max=0.0133, SD=0.0012) for the plots in the study area; (b) Distribution of the plots with a statistically significant contribution to β -diversity (LCBD values: min=0.0100, max=0.0111, SD=0.0003)

ings increased α -diversity in winter wheat, whereas the proportion of forested areas had no influence (Petit et al. 2016). Conversely, the abundance of woody vegetation positively affected α -diversity in our communities. However, this is probably due to extensive agricultural areas hosting more patches of natural vegetation, and not because woody vegetation is a source of species in fields. Our dataset is negligible in the presence of trees, shrubs, and species from woody habitats. Other studies mainly indicate a prevailing effect of local

Table 2 Species Contribution to Beta Diversity (SCBD) values and species frequencies in the dataset for the 40 taxa contributing the most to the β -diversity in our dataset. Taxa are ordered according to decreasing SCBD values. Species of conservation interest in Europe are highlighted in regular bold

Species	SCBD	% Frequency	Species	SCBD	% Frequency
<i>Lolium multiflorum</i>	0.043414	47.6	<i>Anthemis arvensis</i>	0.011875	8.6
<i>Polygonum aviculare</i> agg.	0.036301	47.6	<i>Fallopia convolvulus</i>	0.011725	30.5
<i>Papaver rhoeas</i>	0.031582	73.3	<i>Vicia sativa</i> agg.	0.011394	34.3
<i>Convolvulus arvensis</i>	0.031384	54.2	<i>Sonchus asper</i>	0.011006	25.7
<i>Lysimachia arvensis</i>	0.02872	51.4	Centaurea cyanus	0.010818	5.7
Scandix pecten-veneris	0.02589	27.6	<i>Cirsium arvense</i>	0.010695	21.9
<i>Helminthotheca echioides</i>	0.024161	39.0	<i>Phalaris paradoxa</i>	0.010121	16.2
Galium tricornutum	0.023874	33.3	<i>Coronilla scorpioides</i>	0.009715	18.1
Ranunculus arvensis	0.020315	24.7	Agrostemma githago	0.009441	6.7
<i>Matricaria chamomilla</i>	0.015858	15.2	<i>Bupleurum subovatum</i>	0.008633	12.4
<i>Medicago arabica</i>	0.015609	19	<i>Phalaris brachystachys</i>	0.00857	11.4
<i>Alopecurus myosuroides</i>	0.015138	16.2	<i>Apera spica-venti</i>	0.008458	6.7
<i>Bifora testiculata</i>	0.014542	20	<i>Avena sterilis</i>	0.008181	14.3
<i>Veronica persica</i>	0.01359	32.4	<i>Dasyphyrum villosum</i>	0.007766	9.5
<i>Veronica hederifolia</i>	0.013576	6.67	<i>Poa annua</i>	0.007682	12.4
Adonis annua	0.013504	23.81	<i>Viola arvensis</i>	0.007612	19
Legousia speculum-veneris	0.013468	36.19	<i>Ranunculus sardous</i>	0.007396	5.7
<i>Veronica arvensis</i>	0.013351	20	<i>Lolium rigidum</i>	0.007292	6.7
<i>Sinapis arvensis</i>	0.012724	32.38	<i>Gladiolus italicus</i>	0.007231	18.1
<i>Fumaria officinalis</i>	0.012346	26.7	<i>Cota altissima</i>	0.007062	20

management and limited effects of the surrounding landscape on α -diversity (Ekroos et al. 2010; Bohan and Haughton 2012; Lüscher et al. 2014). Landscape variables affecting arable plants are known to act at a local scale, where finer grain landscapes can increase α -diversity thanks to the abundance of edges and different habitats (Marshall 2009; Gaba et al. 2010). Especially seed rain from other disturbed habitats colonized by annual plants seems to increase the number of species (Gabriel et al. 2005). However, landscape effects were mainly observed in field margins, while the role of management prevails in field cores (Kovács-Hostyánszki et al. 2011). In fact, landscape can be a source of species in field edges, but the features of plant communities in field cores are mainly determined by crop competition and management (Gonthier et al. 2014; Berquer et al. 2021).

The type of rural area had a relevant effect on α -diversity, with more intensive agricultural areas hosting species-poorer plots. This means that traditional, underdeveloped agricultural areas harbor species-richer communities thanks to the survival of traditional, low-input agriculture. In Italy, such traditional agricultural areas host species-rich agroecosystems and are mainly present in hills and mountains (Fanfarillo et al. 2019b). Thus, the negative effect of yearly positive temperatures on α -diversity is likely due to lowlands hosting a more intensive agriculture, rather than to a direct relationship between species richness and warmer climates. Previous evidence highlighted that α -diversity in the study area increases with elevation, the latter being negatively correlated with yearly positive temperature (Fanfarillo et al. 2020b). Similar results emerged from other European Countries (Lososová et al. 2004; Fried et al. 2008; Pál et al. 2013). However, we removed elevation from explanatory variables since it highly correlated with latitude and longitude.

Climate and latitude were the main drivers of species composition, consistently with previous evidence from the study area (Fanfarillo et al. 2020b). Agronomic factors (type of rural area) significantly affected species composition, though explaining a reduced portion of the variance (0.4%), while landscape had no significant effects. Consistently with our findings, geographic location and agricultural management, but not landscape features, explained differences in plant species composition in arable fields of western-central Europe (Lüscher et al. 2014). Likewise, other authors highlighted the importance of biogeographical and environmental factors on the species composition of Eurasian arable plant communities (Lososová et al. 2004; Šilc et al. 2009; Nowak et al. 2015). However, there is evidence that such factors, though important, are subordinate to agricultural practices, highlighting once again the importance of management (Fried et al. 2008; Pál et al. 2013).

The total β -diversity of our communities was significantly explained by all of the four sets of variables. However, agronomic factors and landscape had a minor effect, compared to latitude and climate. This effect of the geographic location and climate, as drivers of environmental heterogeneity, on β -diversity was previously observed in an analysis of arable plant communities in two environmentally very different study areas in Europe (Armengot et al. 2012). In the same study, the diversification of management practices was an important driver of floristic and ecological differentiation among communities. This is consistent with our results, underlying the importance of a multifactor approach in the investigation of arable plant diversity.

Replacement was affected as well by latitude and climate, and it was the component contributing the most to the total β -diversity. This is partially consistent with previous studies in field margins, which showed how temporal changes in β -diversity are related to management and dominated by replacement (Alignier and Baudry 2016). The type of agricultural area had a considerable effect on richness difference. This confirms the importance of the agricultural context in determining the species richness of arable plant communities, though in an indirect way. In fact, fields located in traditional agricultural areas are more likely to be under low-input management than fields located in intensive agricultural areas. Similarly, organic fields are more likely to occur in complex landscapes (Norton et al. 2009).

In our work, high LCBD values effectively detected the arable plant communities being in a bad conservation status, either due to intensive management or to ongoing land abandonment. The former were those containing fewer total and rare/threatened species and being located in intensively managed landscapes, where only generalist and highly competitive species survive (Fried et al. 2010). The latter, though containing many threatened arable plants, were located in abandoned landscapes where arable farming is vanishing and species from natural habitats are recolonizing fields at the expense of arable plant communities (Fanfarillo and Kasperski 2021). As an exception, some plots had high LCBD values due to their location in particular ecological contexts, like wetlands or badlands, without linkages to their conservation status. Overall, the very low number of plots with significantly high LCBD values suggests that most of the arable plant communities of the study area are in a favorable conservation status.

The highest contribution to β -diversity was given by the most frequent species. This could be expected since such species are the ones varying the most in occurrence and abundance. A positive relationship between species frequency and SCBD values was also detected in other studies (Heino and Grönroos 2017).

Implications for arable plant diversity conservation and restoration

Our study revealed a complex situation in which different groups of determinants have varying and synergistic effects on different features of the studied communities. This highlights that, to be successful, conservation measures of arable plant diversity should rely on multifactor approaches, as already supported by more local studies (Seifert et al. 2015). The analysis and partition of β -diversity showed to be a promising tool for the identification of conservation priority sites, which, in this case, are mainly highlighted by the plots having the lowest LCBD values. This evidence can be interpreted as an indicator of the good conservation status of the majority of the surveyed plant communities, consistently with previous expert-based assessments of the status of arable habitats in Italy (Janssen et al. 2016).

Local management seems to play a major role in the conservation of arable plant communities in the study area. Consistently, previous evidence showed that management factors like crop height, tillage depth, preceding crop, or the overall intensity of management are of primary importance in determining species richness, composition, or both (Fried et al. 2008; Pál et al. 2013; Berquer et al. 2021). The restrained effects of landscape features allow us to confirm that agricultural practices, rather than the surrounding landscape, should be the focus for the conservation of arable plant diversity, as previously highlighted on a local scale (Armengot et al. 2011). Even the conservation of refugia on field edges might be ineffective, if whole fields are not appropriately managed. In fact, typical arable weeds are more present in field cores, while they can be outcompeted by species from the immediate landscape on margins (Metcalfe et al. 2019). Thus, we suggest that the maintenance of favorably managed arable habitats is crucial for preventing this kind of biodiversity from disappearance.

In our research, traditional, economically underdeveloped agricultural areas harbored a considerably higher α -diversity in winter arable fields, and also appeared to be the refuge for arable species of conservation interest. This evidence previously emerged from studies on smaller areas (Fanfarillo et al. 2019b; Georgiadis et al. 2022), and we can speculate that it is related to the low intensity of arable farming in such vanishing agricultural contexts. We had signals that some conservation hotspots in central Apennines are disappearing due to land abandonment, as highlighted by the co-occurrence of threatened arable plants like *Adonis flammea*, *Agrostemma githago*, and *Asperula arvensis* and species from semi-natural habitats like *Alyssum alyssoides*, *Cerastium tomentosum*, and *Ranunculus monspeliacus*. Conservation measures should be applied as soon as possible to prevent the alteration and disappearance of such ancient plant communities.

We showed that our study area is a reservoir of arable plant diversity. This is important in the light of the restoration of arable plant communities in areas where they are severely degraded, and where species reintroduction from other areas is necessary to restore original seed banks (Wietzke et al. 2020). In fact, when fields are abandoned or converted to intensive agriculture, seed banks quickly change their composition and the sole re-establishment of favorable management conditions can be ineffective for restoration, especially regarding the recovery of threatened arable plants (Hyvönen 2007; Richner et al. 2018). In this context, our results show that biogeographical features and climatic conditions should not be neglected for planning threatened arable plant species reintroductions, whose success can be highly site-specific (Lang et al. 2021).

Authors' contributions E.F. conceived the research, planned and carried out the field sampling, made landscape photo-interpretation, analyzed the data, made literature search, interpreted the results, and wrote the manuscript. S.M. conceived the research, planned data analyses and the collection of landscape data, interpreted the results, and supervised the research. C.A. and T.F. made data preparation, literature search, and results interpretation. L.d.S. contributed to landscape photo-interpretation and carried out part of the G.I.S. analyses. A.T. and L.R. provided part of the plant community data. G.B. planned and carried out data analyses, interpreted the results, and supervised the research. All authors critically revised the manuscript.

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Data availability All the used data are available upon request to the authors.

Declarations

Conflict of interest The authors declare that they do not have conflicts of interest.

Ethical approval Not applicable.

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