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## Research Article

### Functional diversity in agricultural landscapes: evidence of long-term clustering and multi-scale effects of land use on avian communities

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Functional diversity (FD) is an essential community property connecting biodiversity, ecosystem functioning, and conservation objectives. In agricultural landscapes, avian communities, which play key functional roles, are facing large-scale biodiversity erosion, largely due to land-use changes. However, the long-term spatiotemporal dynamics of FD and its responses to land use remain poorly understood. This study addressed this gap by analysing bird community data collected from lowland agricultural landscapes at a regional scale between 2007 and 2021. We analysed temporal trends in FD metrics (richness, divergence, evenness), their relationships with species richness, changes in functional composition, patterns of clustering/overdispersion, and examined the multi-scale effects of land use across a local-to-landscape gradient. FD metrics were computed using a probabilistic hypervolume approach and standardised against null expectations. Cause–effect relationships were explored using generalized additive models. Results revealed a decline in FD metrics, despite recent recoveries in richness and divergence. Species richness increased linearly and negatively influenced FD metrics. These findings, coupled with evidence of functional clustering, suggested a loss of functions and originality in the functional space, an increase of redundancy, and a shift towards traits associated with forest-dwelling, larger-bodied or omnivorous species. Land use was found to affect FD, likely acting as an environmental filter promoting trait clustering. Built-up areas exerted a detrimental effect on all FD metrics at smaller scales, while arable land increased FD across all scales. Woody features increased FD primarily at the landscape level, while hedgerows showed a reversed effect on evenness. Meadows and shrubs were important to sustain functional divergence at the local scale. Wetlands increased functional richness and divergence without affecting evenness. These findings raise important questions on the relationships between FD and species richness, emphasise the value of long-term data, and highlight the benefit of a multi-scale spatial approach for guiding land-use planning and biodiversity conservation.

Keywords: agricultural landscapes, avian community, functional diversity, land use, spatial scales, trait clustering



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## Introduction

Land-use change is among the main drivers of biodiversity loss worldwide at multiple taxonomical and ecological levels (Newbold et al. 2015, Jaureguiberry et al. 2022). The rising demand of new lands for farming, a key driver of land-use conversion, poses an escalating threat to biodiversity. Furthermore, agricultural intensification has driven significant changes in agricultural landscapes, resulting in the homogenisation and oversimplification of agroecosystems through the spread of monocultures, the industrialisation of farmland practices, and the erosion of natural and semi-natural features (e.g. forest patches, hedgerows, permanent meadows) scattered within the agricultural matrix (Mellanby 1981, Wilson et al. 2009). Moreover, the conversion of natural and agricultural lands into built-up areas is growing at unprecedented rate, and the level of urban lands is expected to reach 4.72% of all the Earth's surface by 2040 (van Vliet et al. 2017). Urbanisation is associated with habitat loss and fragmentation, pollution, and increased human disturbance, representing a serious threat to biodiversity (McKinney 2006, Bani et al. 2022, Tschardtke and Batáry 2023). The persistence of natural and semi-natural areas in agroecosystems is important to sustain the landscape heterogeneity and promote large-scale biodiversity (Tschardtke et al. 2021). For instance, residual forest patches, hedgerows, and shrubs can benefit biological communities in several ways, including provision of refugia, nesting sites and food (Hinsley and Bellamy 2000, Haslem and Bennett 2008). Similarly, water bodies and wetlands may enhance landscape heterogeneity, support diversified ecological functions, providing various benefits for several taxa (Fehlinger et al. 2023, Liao et al. 2024).

In territories of long-history human management, agricultural landscapes can be important environment for biodiversity conservation (Batáry et al. 2015). This is the case of European agricultural lowlands, where biodiversity evolved over millennia of extensive management. Since the 1950s, the industrialisation of agricultural practices has profoundly shaped agroecosystems (Jepsen et al. 2015), contributing to biodiversity loss despite increasing awareness and efforts to implement effective agri-environmental policies (Pienkowski and Pain 1997, Pe'er et al. 2022).

In agroecosystems, avian communities play crucial ecological roles (e.g. seed dispersers, top-down regulation, nutrient cycling, ecosystem engineers), therefore they are a key taxon in maintaining ecosystem functioning (Şekercioğlu et al. 2016). Functional diversity quantifies the distribution of trait-based functional units within a multidimensional space (i.e. the functional space) (Villéger et al. 2008), which allows considering species-specific features and functional roles of species within assemblages, hence linking biodiversity, ecosystem functioning and conservation targets (Cadotte et al. 2011). A trait-based community approach offers several advantages (McGill et al. 2006) and can help the understanding of the mechanisms that underlie the community responses to environmental gradients and ecosystem functioning (Gagic et al.

2015, Peña et al. 2023). From a conceptual framework, community functional diversity consists of three essential metrics, i.e. richness, divergence, evenness (or regularity) (Mason et al. 2005, Mammola et al. 2021, Palacio et al. 2022). Using multiple metrics may be more useful than using a single metric because it can inform about different properties of the functional space, from diversification of functions to redundancy and resilience. Functional diversity, especially functional richness, is expected to be positively influenced by species richness, due to the addition in the community of new species that provide new traits to the functional space (Mouchet et al. 2010). However, assuming that functional diversity metrics are good proxies for niche space and differentiation (Violle and Jiang 2009), an increase of species richness can be associated either with the occupation of novel region of niche space or with a denser packing within the existing niche space (MacArthur 1965, Pellissier et al. 2018). Moreover, functional diversity-species richness relationships can also follow asymptotic functions, suggesting that trait redundancy or the displacement of functionally similar species can occur beyond a threshold (Luck et al. 2013, García-Navas and Thuiller 2020).

In contrast to taxonomic richness (e.g. species richness), there is a gap in knowledge about temporal trends in functional diversity metrics within avian communities (Leroy et al. 2023). Additionally, temporal trends in species richness and functional diversity are neither necessarily coupled nor generalisable; patterns may diverge or align depending on the system or the scale of analysis (Mendez et al. 2012, Barnagaud et al. 2017, Quimbayo et al. 2024). These gaps limit our ability to understand how communities are responding to a changing environment. They hinders the understanding of whether environmental policies are achieving the desired outcomes in terms of ecosystem functioning, and restricts the ability to design studies to identify the drivers of change. Functional clustering, i.e. the observed functional diversity is lower than expected by chance (also referred to as trait underdispersion, in contrast to trait overdispersion; Kraft et al. 2015, Mammola et al. 2024), can commonly occur in agricultural landscapes because less diversified lineages can cope with these human-modified environments (Flynn et al. 2009). However, unexpected patterns may emerge, possibly linked to land uses (e.g. higher proportion of natural vegetation) that can increase the availability of more diversified niche space (García-Navas and Thuiller 2020).

Land use can be among the drivers affecting functional diversity, by promoting environmental filtering or altering resource availability (Martínez-Núñez et al. 2023, Campos et al. 2024). However, even in a well-studied taxon as birds, the effects on functional diversity are still far from being fully understood and are likely to be sensitive to the spatial scale of analysis (Jarzyna and Jetz 2018). Despite the rising effort to understand predictable changes in avian functional diversity in relation to land use at various spatial scales (from global to local; Pringle et al. 2019, Martínez-Núñez et al. 2023, Bouvier et al. 2024, Liao et al. 2024),

our knowledge about the variability in functional diversity metrics along a spatial scale gradient, e.g. from local to landscape scale, remains limited. It is not predictable that an environmental variable, e.g. the percentage of a specific land-use category, will have an effect that is consistent across different spatial scales (Anderle et al. 2022, de Souza Leite et al. 2022). In this context, multi-scale spatial modelling may provide useful insights for landscape planning from a conservation perspective (Rosin et al. 2021, de Souza Leite et al. 2022, Andreatta et al. 2025).

Using data from a long-term breeding bird regional survey in northern Italy, we analysed changes across multiple facets of avian functional diversity in lowland agricultural landscapes, and evaluated how land use affect functional diversity at multiple spatial scales. Specifically, this study aims to: 1) assess the temporal trends in functional diversity metrics (FD), namely richness (FRic), divergence (FDiv), and evenness (FEve), as well as changes in functional composition within communities over 15-year period (2007–2021); 2) analyse the relationships between FD and species richness and compare their trends; 3) evaluate the prevalence of functional clustering or overdispersion for the FD metrics and assess the temporal trends in clustering/overdispersion; 4) analyse the effects of land use on FD metrics and clustering/overdispersion at multiple spatial scales along a local-landscape gradient. In light of these objectives, we hypothesise: 1) decreasing trends in FRic, FDiv and FEve, with a functional reshuffle of community composition towards less-adapted farmland species, in line with their decline at both regional and continental scales (Tirozzi et al. 2021, Rigal et al. 2023); 2) positive associations between FD metrics and species richness (García-Navas and Thuiller 2020); 3) a prevalence of functional clustering rather than functional overdispersion, linked to environmental constraints in intensive agricultural landscapes (Flynn et al. 2009); 4) a negative effect of urbanisation (Sol et al. 2020) and a positive effect of natural and semi-natural features (e.g. shrubs, hedgerows, forest patches, wetlands) on FD across spatial scales (Tschardt et al. 2021).

## Material and methods

### Study area

The study was carried out in a 13 785 km<sup>2</sup> area of the alluvial Po Plain, within the administrative region of Lombardy, northern Italy (45°N, 09°E) (Fig. 1a–b). The territory is predominantly flat (mean=118 m a.s.l., SD=101 m) with a slight elevational gradient increasing from south to north due to transition from the alluvial plain towards hills and mountains at the base of the Prealps. The area is highly anthropized being dominated by agricultural lands and urban areas. Agriculture is mostly intensive, and the main crops are maize, wheat, rice and hayfields (source: National Institute for Statistics [ISTAT], <https://www.istat.it>, accessed on 10 February 2024; Fig. 1c). The mid-west territories are deeply urbanised, where the large city of Milan and its suburban

areas result in a dense urban fabric. Residual forest patches are scattered in the area, mainly around rivers and streams. In the last forty years, the agricultural lands have decreased from 10 950 km<sup>2</sup> in the 1980s (9644 km<sup>2</sup> in 1999) to 9050 km<sup>2</sup> in 2021, essentially due to their conversion into urban areas, which increased from 1642 km<sup>2</sup> in the 1980s (2566 km<sup>2</sup> in 1999) to 3036 km<sup>2</sup> in 2021 (data elaborated from the digital land-cover maps, <https://www.geoportale.regione.lombardia.it>) (Fig. 1d).

### Bird data

Bird data were derived from the Long-term Monitoring Program of Breeding Birds of Lombardy using data collected between 2007 and 2021 (15 years) (Bani et al. 2009, Tirozzi et al. 2021). Surveys were carried out using a standardised method based on a single-visit point-count technique with unlimited distance (Blondel et al. 1981) according to a stratified random design. All birds heard or seen in 10 min were recorded (Fornasari et al. 1998) and counts were expressed as number of breeding pairs according to the method described in Blondel et al. (1981). Surveys were performed between 10 May and 20 June, from sunrise to 11.00 a.m., only in good weather conditions. To analyse lowland farmland communities, we retained point counts only performed in lowland (altitude ≤ 350 m a.s.l.) agricultural landscapes, i.e. point counts with at least 50% of agricultural land use (including all types of agricultural land) within a 1000-m radius circular buffer around the sampling point in its first year of sampling (e.g. 2007 if the first sampling occurred in 2007, 2008 if the first sampling occurred in 2008 and so on; Supporting information). From this data selection, we only retained point counts performed into agricultural sampling locations, i.e. those sites with at least 60% of agricultural land use within a 250-m radius buffer in the first year of sampling as described above. This prevented the retention of sites falling within agricultural landscapes but situated in non-agricultural locations at site level (e.g. residual forest patches, towns).

Considering that the survey data include both annually randomly extracted (i.e. non-permanent) and fixed (i.e. yearly repeated point counts at the same location) point counts, for the temporal trend analyses, functional clustering/overdispersion, relationships between FD and species richness, we only used fixed point counts with at least five repetitions over the whole time series, i.e. time coverage ≥ 33% (dataset Dfix). Conversely, for the analyses about the relationships between FD metrics and land-use features, we used both fixed and non-permanent point counts (dataset Dfix\_ran). Therefore, trend analyses were conducted using only fixed point counts with at least five years of repeated sampling, whereas land-use models used a larger dataset that included both fixed and non-permanent point counts. In both datasets, we excluded from the analyses very rare or erratic species (overall relative frequency less than 0.5%), species that might not be properly monitored by the survey (nocturnal raptors, aquatic birds) and gulls because of the presence of non-breeding vagrant individuals.

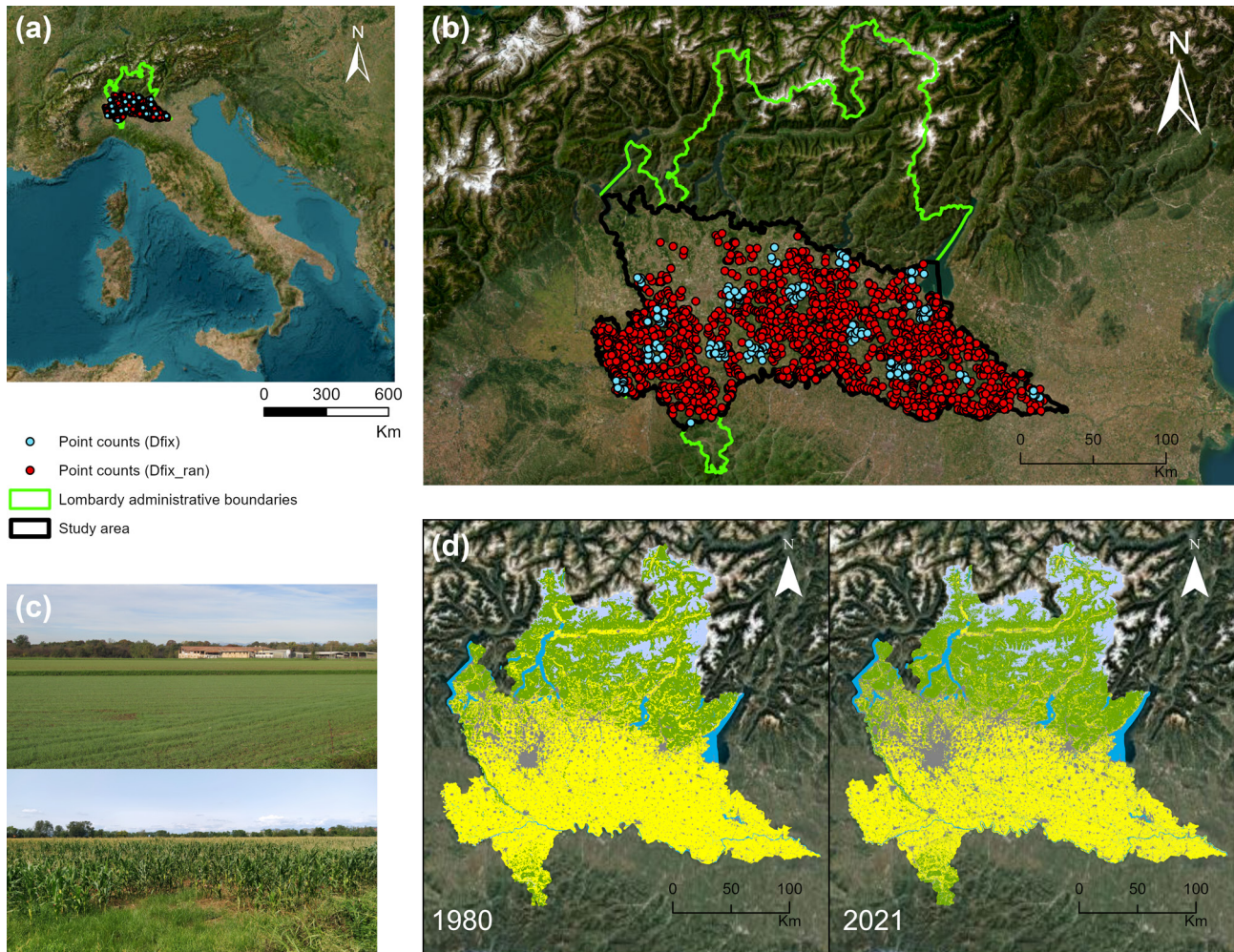


Figure 1. Study area. Location of the study area with the surveyed sites (a, b). Pictures of typical agricultural landscapes in the area (c). Comparison of land uses between 1980 and 2021 (grey = urban cover, yellow = agricultural cover, green = natural and seminatural cover, light blue = non-vegetated natural cover, blue: water bodies; data elaborated from DUSAF maps) (d).

### Avian traits

We compiled 17 avian traits from information collected in Pearman et al. (2014), Wilman et al. (2014), Storchová and Hořák (2018) and AVONET (Tobias et al. 2022). The selected traits summarised information on the life history and ecological features of the species and included: body weight (numerical), mean clutch size (numerical), number of broods per year (numerical), hand-wing index (numerical), nest type (categorical; five levels), primary habitat (categorical; six levels), main diet (categorical; five levels), foraging behaviour (categorical binary; four traits), and foraging substrate (categorical binary; six traits). The full Species  $\times$  Trait matrix along with details on traits is provided in the Supporting information.

### Functional diversity metrics

Considering traits encompassed categorical, binary and continuous traits, we used the Gower's distance (Gower 1971, Pavoine et al. 2009) to transform the trait matrix (i.e. original traits) into a dissimilarity distance matrix and then summarised

this dissimilarity matrix using the principal coordinates analysis (PCoA). The PCoA is a metric multidimensional scaling method that summarises distances/dissimilarities of a matrix into a reduced set of orthogonal dimensions. We retained the first four axes of PCoA (Mammola and Cardoso 2020) and assess functional space quality using the mean squared deviation (mSD). The mSD is based on the comparison between the initial and the final distances for each pair of species in the multidimensional trait space (Supporting information); mSD is zero when the functional space perfectly represents the initial distance for all pairs of species and it increases when some pairs of species are poorly represented in the functional space (Maire et al. 2015). To ease interpretation, functional space quality was also expressed on a standardised scale [0–1] using the function *hyper.quality* in the R package 'BAT' (Cardoso et al. 2023). To compute the functional space, we used the multi-dimensional probabilistic hypervolume approach (Blonder et al. 2014, Mammola and Cardoso 2020), which uses kernel density estimators (Blonder et al. 2014, Mammola et al. 2021). The hypervolume approach,

although more computationally demanding, offers several advantages over other methods, such as functional dendrograms or the widely used convex hull approach. Notably, it allows for the incorporation of species abundance into the assessment of functional space, is less sensitive to species outliers, and enables the detection of regions with higher or lower density within the trait space, thus allowing for the representation of uneven probabilities of finding species with a given trait combination throughout the boundaries of functional space (Blonder 2016, Mammola and Cardoso 2020). To construct hypervolumes, we used a Gaussian kernel density estimator with the Silverman method for the bandwidth estimation and the default probability threshold (0.95) (Blonder et al. 2018). The observations with fewer than three species (one in Dfix, and four in Dfix\_ran) were excluded due to potential issues (zero value) in kernel bandwidth estimation (*hypervolume\_gaussian* function of 'hypervolume' package; Blonder et al. 2023). The hypervolume construction was weighted by the species relative abundance (normalised values within species). We then estimated three FD metrics: 1) functional richness (FRic), i.e. the total volume of the hypervolume; 2) functional divergence (FDiv) as the average pairwise distance of a sample of stochastic points in the hypervolume; 3) functional evenness (also referred as regularity, FEve) as the overlap between the estimated hypervolume and a theoretical hypervolume where trait and species occurrences are evenly distributed within their possible range (Carmona et al. 2016, 2019, Mammola and Cardoso 2020). For each FD metric and each observation (i.e. an assemblage at any site and time), we calculated the standardised effect size (SES) as the difference between the observed FD metric and the mean of its null distribution, divided by the SD of the null distribution:  $SES = [\text{Obs}(\text{FD}) - \text{mean}(\text{FD}_{\text{null}})] / \text{SD}(\text{FD}_{\text{null}})$ . The null distribution was generated by calculating the expected FD metric from a random assembly (1000 simulations for each observation) while keeping observation-level species richness constant (Palacio et al. 2022). Therefore, the SES indicates the extent to which the FD metric in a real community deviate from expectations under a null model, while taking species richness into account. Hypervolumes and FD metrics were computed using the 'BAT' package (Cardoso et al. 2023) in R ([www.r-project.org](http://www.r-project.org)). The matrix was randomised using the R package 'picante' (Kembel et al. 2010), and the computations were performed using the CINECA High-Performance Computer Leonardo (<https://www.hpc.cineca.it/systems/hardware/leonardo/>).

Functional trait space and FD metrics were computed separately for the two datasets (Dfix, Dfix\_ran) to prevent the inclusion of species occurring below the frequency threshold or that were never observed at any site and time within each dataset.

Additionally, to assess changes in functional composition within communities over time, we calculated the community-weighted mean (CWM) (Garnier et al. 2004, Ricotta and Moretti 2011) for the Dfix dataset. CWM is defined as the mean trait value within an assemblage, weighted by species abundance (normalised values within species), and

was computed using the *cwm* function in the 'BAT' package. CWM is widely used to capture variation in individual traits and to describe trait syndromes (Hahs et al. 2023, Zheng et al. 2025).

### Functional clustering/overdispersion

To compare the observed values of the FD metrics with values expected by chance, we firstly checked for skewness of the null distributions; considering that null distributions deviated from a symmetric distribution (Supporting information), we considered values lower than the 2.5% and higher than 97.5% of the null distributions as lower or higher than expected by random assemblages given species richness (Palacio et al. 2022). Then, we calculated the associated p-values representing the probability to observe lower or higher values than a random expectation, i.e. functional clustering or overdispersion of traits, respectively. One-tail tests ( $\alpha=0.05$ ) were computed whether there was clear evidence of unidirectional deviation from the null distributions.

### Modelling temporal trends in FD metrics, clustering/overdispersion, and community-weighted mean

Generalised additive mixed models (GAMMs; Hastie and Tibshirani 1986, Wood 2017) were used to model the trajectory of each FD metrics (we used the SES as responses variables with a Gaussian error distribution) over time (2007–2021). A random intercept was included as random nested effect to take into account the correlation structure of clustered point counts within primary sampling unit over time ('point count ID' nested in 'Primary sampling unit'), and the year of sampling was modelled as fixed effect by using a thin plate regression spline (maximum degree of freedom set at three, i.e.  $k=4$ ). Restricted maximum likelihood (REML) was used as smoothing parameter estimation method (Wood 2011, 2017). In addition, a temporal autocorrelation of order 1 (AR1) was initially included in the models; however, considering that the autocorrelation function (ACF) for model residuals did not show substantial changes when comparing the models with AR1 function with those without it, we excluded the AR1 from the final models. Residuals were checked to verify statistical assumptions of mixed models and GAMMs (Wood 2017, Pinheiro and Bates 2000). GAMMs were fitted using the 'mgcv' package (Wood 2023) in R. The same framework was applied to assess the temporal trend for the community-weighted means of traits (standardised values, Gaussian error distribution) and for functional clustering or overdispersion (i.e. the probability of clustering/overdispersion, binomial error distribution; Supporting information).

### Relationships between FD metrics and species richness

To explore the relationships between species richness and FD metrics (FRic, FDiv, FEve), using the Dfix dataset, we first correlated species richness with FD metrics (SES) by means of Pearson's correlations for each community-level observation. Then, we developed GAMMs with a random structure as for the temporal trend models presented above, fitted by

REML and using a thin plate regression spline ( $k=4$ ) to model potential non-linear relationships. In these models, the SES of each FD metric was the response variable (Gaussian error distribution), and the species richness was the explanatory variable.

## Relationships between FD metrics and land use at multiple spatial scales

### Environmental covariates

Land-use fractional cover and hedgerows' density were calculated from the digital land-use maps named 'DUSAF' and the 'hedgerows' maps' of the Lombardy region available for years 2007, 2012, 2015, 2018, 2021 (downloadable at <https://www.geoportale.regione.lombardia.it/>, accessed on 6 February 2024). To describe a local–intermediate–landscape gradient, we used three distance radii, namely 100, 500 and 2000-m. For land uses (built-up areas, arable land, rice fields, cultivated meadows (hereafter meadows), orchards, timber plantations, shrubs, forests, water bodies and wetlands, Supporting information) we calculated the percentage of cover within each circular buffer around bird point counts for each distance radius. Hedgerows' density was calculated by a kernel density estimator to calculate the density as linear km/square km within each radius. For both land-use fractional covers and hedgerows' density, the annual bird point counts were associated to the temporally closest values (Supporting information). The spatial analyses were computed in ArcGIS ver.10.8.2 (ESRI 2019) and R ([www.r-project.org](http://www.r-project.org)).

### Multi-scale regression models

To assess the relationships between FD and land use, we developed a generalised additive model (GAM) at three spatial scales, namely 100-m (local), 500-m (intermediate), and 2000-m (landscape) radii buffers (hereafter referred as 100, 500 and 2000-m, respectively) using the SES of the metric (with a Gaussian error distribution) or the probability of clustering/overdispersion (with a binomial error distribution) as response variable. These radii were selected to reflect bird territory sizes (Schifferli 2001) and to capture scale-dependent community responses along a local-to-landscape gradient (Rosin et al. 2021, de Souza Leite et al. 2022, Bouvier et al. 2024). GAMs were fitted using the package 'mgcv' (Wood 2023) in R. For all the explanatory variables, we used the thin plate regression spline as method of smoothing and penalised the smoothing process through the shrinkage method in order to avoid overfitting and exclude non-significant variables by decreasing the level of the estimated degrees of freedom close to zero (Wood 2017). To guarantee a reasonable ecological interpretation, we set the maximum possible effective degree of freedoms (edf) at two (i.e.  $k=3$ ). To control for potential temporal and spatial autocorrelation we also include a space-time smoother resulting from the interaction among latitude, longitude (WGS84 datum) and year of survey (Harrison et al. 2014). The space-time smoother was handled as a full tensor product applying the shrinkage and setting the maximum edf to 26 (i.e.  $k=3$  for each interacting

variable; Tirozzi et al. 2024). We used the restricted maximum likelihood (REML) as the smoothing parameter estimation method (Wood 2011, 2017). The analysis of concurvity (i.e. the equivalent of collinearity in GAMs) showed that the inclusion of rice fields highly increased the level of concurvity in all the models, therefore we removed this variable, and no further significant problems were detected (Supporting information). Diagnostic plots of residuals were inspected to verify the absence of violations in model assumptions. For each FD metric, models were ranked using delta AIC (Burnham and Anderson 2002) to identify the best fitting. All models were reported and discussed.

## Results

### Communities' composition and functional space

We analysed 1562 and 3102 assemblages in 151 and 1587 distinct sites for the dataset Dfix (only fixed point counts) and Dfix\_ran (both fixed and non-permanent point counts), respectively (104 and 207 surveyed sites per year on average,  $SD=24$  and  $63$ , respectively). We detected a total of 71 species, belonging to 14 orders and 34 families, in both datasets, with an average of 12 (Dfix) and 11 (Dfix\_ran) species per point count (min–max=3–26 in both Dfix and Dfix\_ran). In both datasets, the most common species was the hooded crow *Corvus cornix* (occurring at 87 and 84% of the total point counts in Dfix and Dfix\_ran, respectively) while the least frequent species were the Montagu's harrier *Circus pygargus* in Dfix, and the black redstart *Phoenicurus ochruros* in Dfix\_ran (0.5% of the point counts). The quality of the functional spaces [range 0–1] was high and essentially identical in both Dfix (0.806) and Dfix\_ran (0.805), with a  $mSD=0.004$  in both cases (Supporting information). The first four axes explained 63% (Dfix) and 62% (Dfix\_ran) of the total variance (Axis 1: 26% in Dfix and 25% in Dfix\_ran, Axis 2: 20%, Axis 3: 9%, Axis 4: 8% in both Dfix and Dfix\_ran). The PCoA plots are provided in the Supporting information. Functional interpretation of the PCoA axes was similar between Dfix and Dfix\_ran datasets. Specifically, Axis 1 was linked to body weight, hand-wing index, clutch size, foraging behaviour (foliage glean), foraging substrate (canopy, shrubs, vegetation), primary habitat, main diet, and, to a lesser extent, nest type. Axis 2 was associated with hand-wing index, body weight (in Dfix), clutch size (in Dfix\_ran), foraging behaviour (sally, pursuit/pounce, graze/pick-peck-stab/dig/overturn object/probe), and foraging substrate (air). Axis 3 was linked to hand-wing index, foraging behaviour (sally), and foraging substrate (ground/mud); Axis 4 was linked to number of broods per year, clutch size, foraging substrate (water), and main diet.

### Observed FD versus null model FD

In the Dfix dataset, across all observations and over the whole period, the mean SES was  $-0.656$  ( $SD=0.790$ ) for the FRic,  $-0.922$  ( $SD=0.987$ ) for the FDiv, and  $-0.714$  ( $SD=0.797$ ) for the FEve. Overall, the observed FRic, FDiv

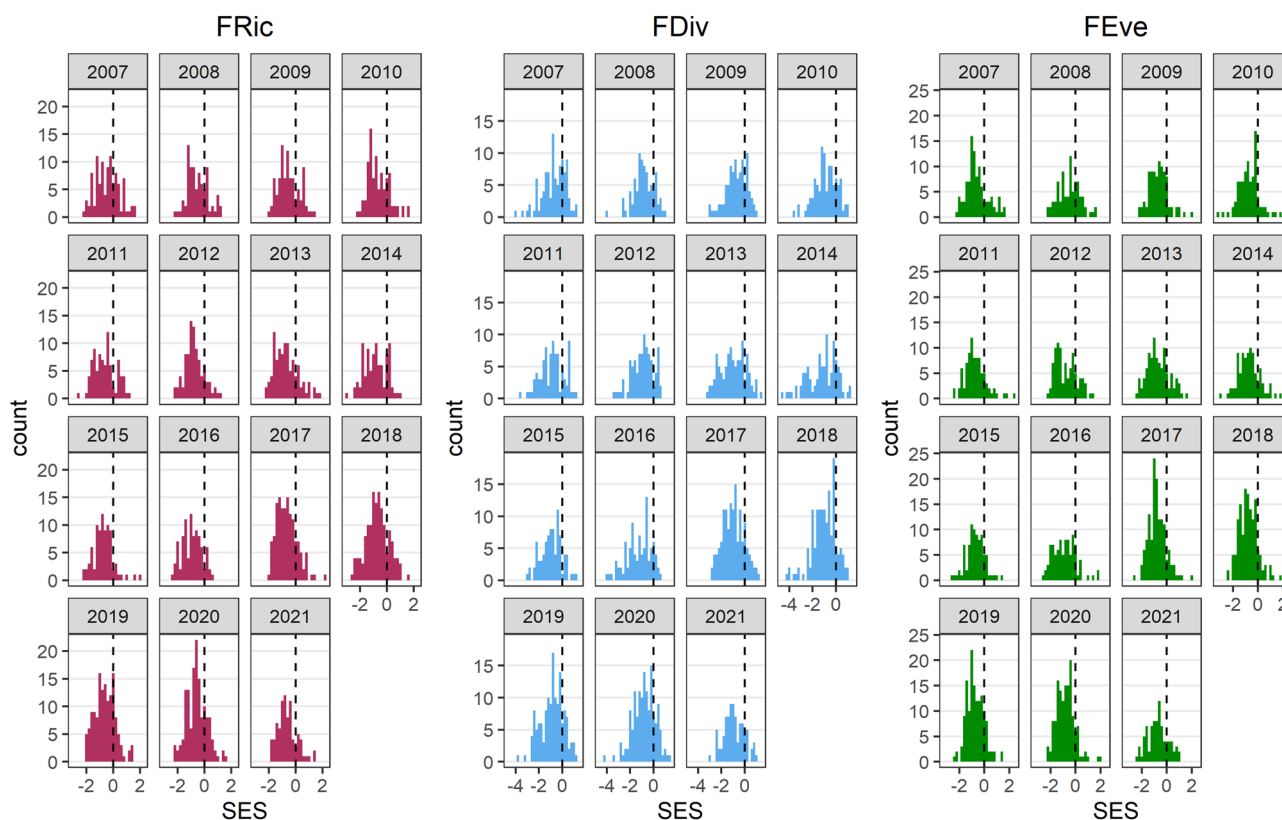


Figure 2. Histograms of the standardised effect sizes (SESs) for the functional richness (FRic), divergence (FDiv) and evenness (FEve) grouped by each year of the time series and across all assemblages. Black dashed lines (zero value) represent the SES when the observed value for FRic, FDiv and FEve is equal to the mean of the null distribution. For each community-level observation, SES were calculated based on 1000 randomisations. Results shown are based on the Dfix dataset, which includes only fixed point counts with at least five years of repeated sampling.

and FEve showed lower values than those expected in random assemblages given species richness within years (Fig. 2). We found a statistically significant difference ( $p$ -value  $\leq 0.05$ , i.e. the observed FD metric was lower than 2.5th percentile or higher than 97.5th percentile of the null distribution) of the observed FD metrics from those expected in random assemblages in 104 (7%), 165 (11%), and 95 (6%) out of the 1562 communities for FRic, FDiv and FEve, respectively. In all these cases (only a single exception for FEve), we found that the observed FD metrics were always lower than a random expectation. Considering this, by testing the only hypothesis that the observed FD index was lower than the 5th percentile of the null distribution ( $\alpha=0.05$ , one-tail test), we found statistical significance in 208 (13%), 296 (19%), and 195 (12%) out of the total assemblages for FRic, FDiv and FEve, respectively (Supporting information). Moreover, across the 151 distinct sites, the 58% (FRic), 68% (FDiv), 54% (FEve) of them showed lower values than random ( $\alpha=0.05$ , one-tail test) at least once (Supporting information).

### Temporal trends in FD metrics, in functional clustering, and in community-weighted mean

Diagnostic plots of residuals were satisfying in all models and did not show any violations of statistical assumptions.

Functional richness, divergence and evenness (SES) showed non-linear trajectories. Richness and divergence firstly declined, then a recovery was detected since 2015 and 2016 respectively. Evenness showed a decline especially in the first period of the time series without evidence of recovery (Fig. 3a–b). Consistently with the temporal trends in the SESs, in the case of FRic and FDiv the probability of observing a functional clustering showed a non-linear temporal trend (initially increase, then decreasing), while for FEve the trend, albeit in increase, was not significant (Supporting information). Additionally, the temporal trend in species richness was also analysed using the same approach adopted for FD metrics (GAMMs), revealing, unexpectedly, a linearly increasing trend over time (edf=1,  $p < 0.001$ ; inset plot in Fig. 3b).

Temporal trends in community-weighted means (CWMs) revealed shifts in functional composition towards assemblages characterised by increasing values of body mass, forest habitat dwellers, omnivorous diet, arboreal nesting, and canopy and vegetation foragers. Simultaneously, communities exhibited declines in values of clutch size, grassland habitat dwellers, seed-based diet, nest types (ground, hole, other), foraging behaviour grouping the levels 'graze', 'pick-peck-stab', 'dig', 'overturn object', 'probe', and foraging substrate comprising

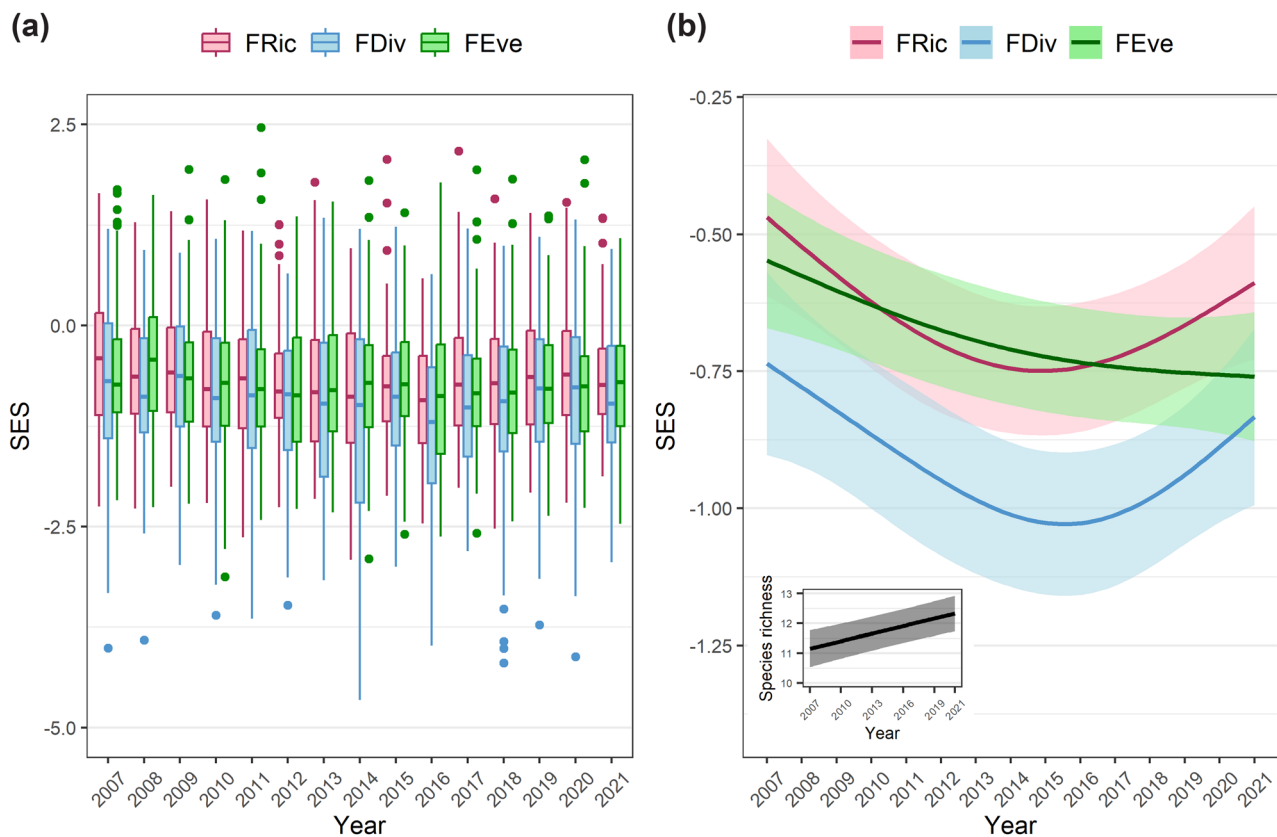


Figure 3. Temporal trends with boxplots in (a) and regression curves (fitted values: solid lines, 95% confidence intervals: shaded area) fitted by GAMMs in (b) for the standardised effect sizes (SESs) for the functional richness (FRic), divergence (FDiv), and evenness (FEve) over the study period (2007–2021). Both (a) and (b) are plotted on the response scale of the SES. In the inset plot in (b), the temporal trend in species richness is showed. Results shown are based on the Dfix dataset, which includes only fixed point counts with at least five years of repeated sampling.

ground/mud, air and water foragers. Traits showing decreasing–increasing trends included invertebrate diet, ground-closer nesters, shrub-habitat dwellers and ‘pursuit/pounce’ foraging behaviour (Fig. 4, Supporting information).

### Relationships between FD metrics and species richness

FRic, FDiv and FEve (SES) showed negative correlations with species richness (Pearson’s  $r$ : FRic =  $-0.19$ ; FDiv =  $-0.14$ , FEve =  $-0.15$ ;  $p \leq 0.001$  in all cases). Moreover, GAMMs showed negative asymptotic relationships in the case of FRic and FDiv, and a linear negative relationship for the FEve (Fig. 5).

### Effects of land use on FD metrics and functional clustering at multiple spatial scales

In the Dfix\_ran dataset, across all observations and over the whole study period, the mean SES was  $-0.589$  (SD =  $0.813$ ) for the FRic,  $-0.817$  (SD =  $0.990$ ) for the FDiv, and  $-0.334$  (SD =  $0.818$ ) for the FEve. Diagnostic plots of residuals were satisfying in all models and did not show any violations of statistical assumptions. Overall, the models explained a moderate proportion of deviance (FRic: 9–10%; FDiv: 7–8%;

FEve: 3–5%). The relationships between FD metrics (SES) and land uses at the three spatial scale are summarised in Table 1, and partial effect plots are reported in the Supporting information. The shape of these response functions was mainly linear. Built-up areas showed negative effects at the 100 and 500-m scales for all FD metrics (also at 2000-m for FEve). Conversely, arable land showed positive effects across all scales and all FD metrics, with the only exception for FEve at the 100-m scale. Meadows showed positive effects on FDiv at the 100 and 500-m scales. Orchards showed negative effects for FRic at the 100- and the 500-m scales, while a positive effect was detected on FEve at the 2000-m scale. Timber plantations had positive effects across all scales and all FD metrics. The effect of forest cover (positive and linear) was significant at the 2000-m scale for all the FD metrics (on FRic it was also detected at the 500-m scale). Hedgerows’ density ( $\text{km km}^{-2}$ ) had a positive effect on FRic and FDiv at the 2000-m scale (on FRic also at the 500-m similarly to forest cover), while it had a negative effect on FEve at the 500-m and the 2000-m scales. Shrub cover showed a positive effect at the 100-m scale on FDiv and FEve, while the effect was negative at the 2000-m scale on FRic and FDiv. Wetlands had positive effects across all scales for FRic and

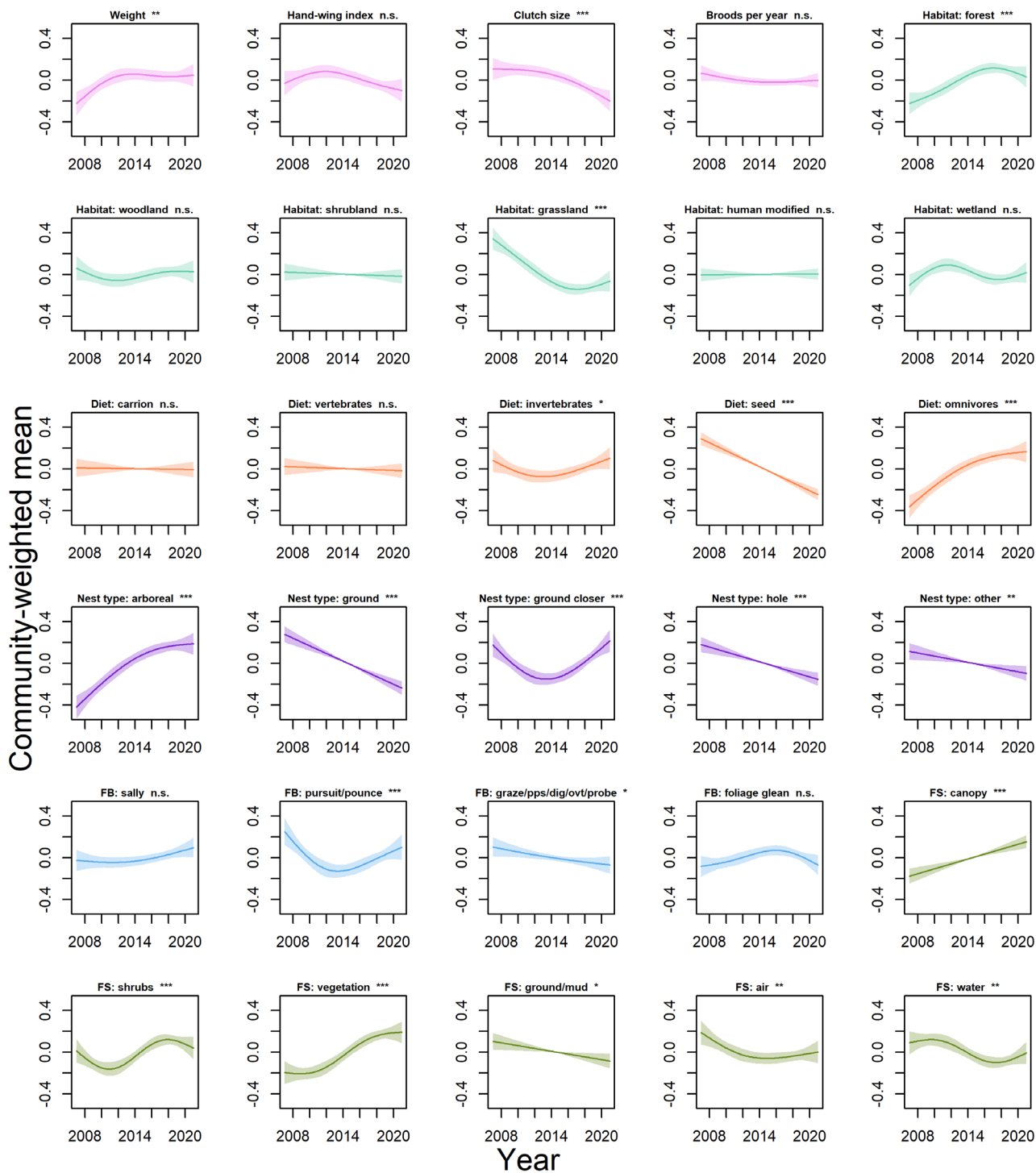


Figure 4. Temporal trends in community-weighted mean (CWM) for each trait (and level, in case of categorical traits) considered in the computation of the functional space. CWM values were standardised prior to modelling, and regression curves are centred around zero enabling direct comparison of trend magnitudes among traits. Plots are colour-coded by trait group: pink – life-history traits; aquamarine – primary habitat; light red – main diet; purple – nest type; light blue – foraging behaviour (FB); olive green – foraging substrate (FS). For full details on traits refer to the Supporting information. N.s. = not significant;  $0.01 < p \leq 0.05$ ; \*,  $0.001 < p \leq 0.01$ ; \*\*,  $p \leq 0.001$ ; \*\*\*. Results shown are based on the Dfix dataset, which includes only fixed point counts with at least five years of repeated sampling.

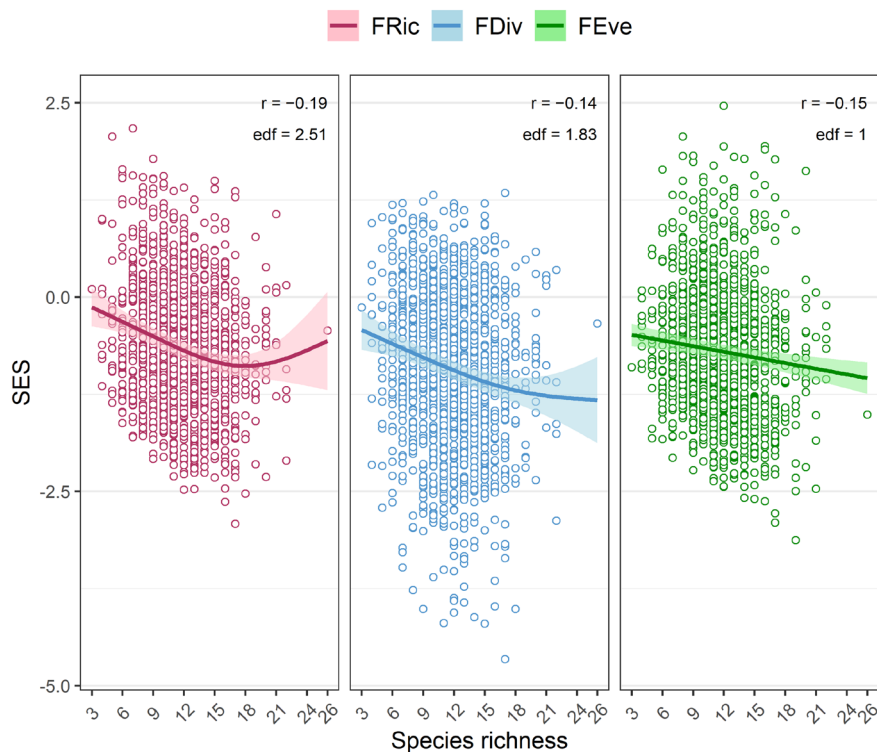


Figure 5. Relationships between standardised effect sizes (SESs) and species richness for functional richness (FRic), divergence (FDiv) and evenness (FEve). Regression curves are derived from GAMMs, dots represent the observed SES. The Pearson's correlation coefficient ( $r$ ) and the effective degree of freedom ( $edf$ ) resulting from GAMMs are reported. For all metrics, both correlations and the effects of species richness were significant. Results shown are based on the Dfix dataset, which includes only fixed point counts with at least five years of repeated sampling.

FDiv, while no effects were found for FEve, yet. For FRic and FEve, the best-supported models by AIC were at the 500-m scale (even though for FRic this was less evident in the 100-m model wherein  $\Delta AIC = 5.76$ ), while for FDiv, the 100 and 2000-m models were equally supported ( $\Delta AIC = 1.49$  for the 2000-m model).

Models on functional clustering (models' summary and partial effect plots in the Supporting information) confirmed, in several cases, the relationships with land use that were observed for the SESs. However, there were some differences. Specifically, no significant effect on FRic was found for arable land and orchards. For meadows, positive effects on functional clustering were found for FEve at the 100 and 500-m scales. For wetlands, a negative effect on clustering, also for FEve, was only detected at the 2000-m scale.

## Discussion

### Temporal trend in FD metrics, functional clustering, community-weighted mean and species richness

Functional diversity is a critical property of biological communities due to its link with ecosystem functionalities (Cadotte et al. 2011). We found that functional diversity in breeding avian assemblages of lowland agricultural landscapes have had non-stationary trajectories over 15

years (2007–2021) at a regional scale. At the same time, it is valuable to notice the linear increase in species richness over the same period. In the study area (Lombardy region), farmland bird populations have decreased in the last three decades, while forest species have increased (Tirozzi et al. 2021). Considering that our pool of species included all those occurring in agricultural landscapes, where various types of habitats are present, it is possible that forest species have benefited from increasing populations, especially in hilly and mountains areas, and successfully colonise forest residual patches in agricultural landscapes (Tirozzi et al. 2022), probably in accordance with a source–sink dynamic, resulting in an increase in species richness. Meanwhile, the study region experienced a significant increase in built-up areas especially to the detriment of agricultural lands. This may have contributed to an increase in species richness due to the colonisation by human-associated or synanthropic species such as Corvidae and Columbidae (Abou Zeid et al. 2023). However, the decrease in functional richness, i.e. a reduction of the volume of the functional space, coupled with the linear increase in species richness suggested that the loss of functionalities cannot be a consequence of a taxonomic rarefaction. This means that the addition of new taxonomic entities could not compensate the loss of species with more diverse range of traits, suggesting an increase of species with more similar traits (Jarzyna and Jetz 2018). Indeed, looking at functional

Table 1. Summary of GAMs for the effects of land uses on the SES for the functional richness (FRic), divergence (FDiv), and evenness (FEve) at the three spatial scales. In each model, the reference degree of freedom of the tensor product for the smoothed interaction between latitude, longitude, and year of sampling was set at 26. For land uses, the maximum effective degree of freedom was set at two. Edf=effective degree of freedom for the smooth terms; F=F-statistic; p=p-value; E=direction of the effect (positive or negative) for land-use variables having a statistically significant effect (marked in bold). Results shown are based on the Dfix\_ran dataset, which includes both fixed and non-permanent point counts.

Spatial scale (m)	Variable	FRic				FDiv				FEve			
		edf	F	P	E	edf	F	P	E	edf	F	P	E
100	Latitude:Longitude:Year	14.72	6.49	< 0.001		15.17	5.87	< 0.001		9.08	1.02	< 0.001	
	Built-up areas	<b>1.14</b>	<b>35.73</b>	<b>&lt; 0.001</b>	–	<b>1.54</b>	<b>12.94</b>	<b>&lt; 0.001</b>	–	<b>0.96</b>	<b>6.73</b>	<b>&lt; 0.001</b>	–
	Arable land	<b>1.75</b>	<b>5.31</b>	<b>0.001</b>	+	<b>1.35</b>	<b>6.69</b>	<b>&lt; 0.001</b>	+	0.58	0.67	0.117	
	Meadows	0.60	0.73	0.111		<b>0.90</b>	<b>3.54</b>	<b>0.004</b>	+	0	0	0.942	
	Orchards	<b>0.80</b>	<b>1.99</b>	<b>0.022</b>	–	0.13	0.08	0.269		0	0	0.752	
	Timber plantations	<b>0.85</b>	<b>2.67</b>	<b>0.011</b>	+	<b>0.94</b>	<b>5.91</b>	<b>&lt; 0.001</b>	+	<b>1.01</b>	<b>17.45</b>	<b>&lt; 0.001</b>	+
	Shrubs	0	0	0.309		<b>0.92</b>	<b>5.24</b>	<b>0.001</b>	+	<b>0.88</b>	<b>3.67</b>	<b>0.004</b>	+
	Hedgerows' density	0.04	0.02	0.306		0	0	0.848		0	0	0.540	
	Forests	0.01	0	0.444		0.01	0	0.519		0	0	0.388	
	Water bodies and wetlands	<b>0.93</b>	<b>6.04</b>	<b>&lt; 0.001</b>	+	<b>0.90</b>	<b>4.53</b>	<b>0.001</b>	+	0	0	0.415	
500	Latitude:Longitude:Year	13.39	5.69	< 0.001		14.33	5.22	< 0.001		11.17	1.76	< 0.001	
	Built-up areas	<b>1.85</b>	<b>28.58</b>	<b>&lt; 0.001</b>	–	<b>1.04</b>	<b>6.78</b>	<b>&lt; 0.001</b>	–	<b>1.06</b>	<b>11.01</b>	<b>&lt; 0.001</b>	–
	Arable land	<b>1.27</b>	<b>9.15</b>	<b>&lt; 0.001</b>	+	<b>1.19</b>	<b>9.46</b>	<b>&lt; 0.001</b>	+	<b>0.94</b>	<b>2.98</b>	<b>0.005</b>	+
	Meadows	0.57	0.67	0.114		<b>0.85</b>	<b>2.56</b>	<b>0.011</b>	+	0.53	0.56	0.134	
	Orchards	<b>0.80</b>	<b>1.94</b>	<b>0.023</b>	–	0.47	0.44	0.156		0.47	0.44	0.152	
	Timber plantations	<b>0.82</b>	<b>2.23</b>	<b>0.018</b>	+	<b>0.91</b>	<b>4.48</b>	<b>0.001</b>	+	<b>1.64</b>	<b>30.10</b>	<b>&lt; 0.001</b>	+
	Shrubs	0	0	0.862		0	0	0.515		0	0	0.884	
	Hedgerows' density	<b>0.89</b>	<b>2.81</b>	<b>0.009</b>	+	0.01	0	0.346		<b>0.92</b>	<b>3.62</b>	<b>0.003</b>	–
	Forests	<b>0.92</b>	<b>4.86</b>	<b>0.001</b>	+	0.72	1.28	0.055		0	0	0.489	
	Water bodies and wetlands	<b>0.82</b>	<b>2.16</b>	<b>0.019</b>	+	<b>0.93</b>	<b>5.57</b>	<b>&lt; 0.001</b>	+	0.20	0.12	0.259	
2000	Latitude:Longitude:Year	14.43	6.66	< 0.001		15.18	6.83	< 0.001		10.87	1.45	< 0.001	
	Built-up areas	0	0	0.497		0.01	0	0.422		<b>0.70</b>	<b>1.08</b>	<b>0.049</b>	–
	Arable land	<b>1.24</b>	<b>9.93</b>	<b>&lt; 0.001</b>	+	<b>1.80</b>	<b>10.35</b>	<b>&lt; 0.001</b>	+	<b>1.16</b>	<b>4.86</b>	<b>&lt; 0.001</b>	+
	Meadows	0	0	0.782		0	0	0.615		0.42	0.36	0.173	
	Orchards	0.52	0.53	0.139		0.06	0.03	0.290		<b>0.74</b>	<b>1.44</b>	<b>0.041</b>	+
	Timber plantations	<b>0.93</b>	<b>4.87</b>	<b>0.001</b>	+	<b>0.90</b>	<b>3.86</b>	<b>0.003</b>	+	<b>1.06</b>	<b>19.71</b>	<b>&lt; 0.001</b>	+
	Shrubs	<b>0.95</b>	<b>7.97</b>	<b>&lt; 0.001</b>	–	<b>0.94</b>	<b>6.40</b>	<b>&lt; 0.001</b>	–	0	0	0.488	
	Hedgerows' density	<b>1.08</b>	<b>5.15</b>	<b>0.001</b>	+	<b>0.90</b>	<b>2.45</b>	<b>0.015</b>	+	<b>0.85</b>	<b>2.06</b>	<b>0.019</b>	–
	Forests	<b>1.12</b>	<b>28.32</b>	<b>&lt; 0.001</b>	+	<b>1.04</b>	<b>15.31</b>	<b>&lt; 0.001</b>	+	<b>0.94</b>	<b>5.24</b>	<b>&lt; 0.001</b>	+
	Water bodies and wetlands	<b>0.98</b>	<b>10.97</b>	<b>&lt; 0.001</b>	+	<b>0.99</b>	<b>11.51</b>	<b>&lt; 0.001</b>	+	0	0	0.645	

divergence and evenness, they have decreased over time following a similar (divergence) or linear (evenness) trajectory. Divergence is an indicator of originality and uniqueness; a lower evenness indicates a lower regularity in traits distribution within the functional space and therefore a higher redundancy. Together, these results suggested a decrease in functional dissimilarity and an increase in functionally redundant species due to a simultaneous increase in species richness and a loss of functionalities (decrease in functional richness). Temporal trends in community-weighted means (CWMs) indicated a directional reorganisation of avian functional composition, favouring traits associated with forest-dwelling, larger-bodied or omnivorous species. Concurrently, communities have experienced a decline in species typical of grasslands and other managed environments, such as the Eurasian skylark *Alauda arvensis* and the western yellow wagtail *Motacilla flava*. In addition, there was a decline in traits associated with ground or cavity nesting, foraging on ground, in air and in water, seed-based diets, or foraging behaviours

involving active manipulation to access food items (e.g. grazing, pick-peck-stab, digging, overturning objects, probing). These findings, aligning with the observed declines of typical farmland birds at regional and continental level (Tirozzi et al. 2021, Rigal et al. 2023), support a functional impoverishment of avian assemblages in agricultural landscapes, with a shift towards pool of species with omnivorous diet or better adapted to structurally complex vegetation. However, in the last years of the time series, both the functional richness and divergence showed a recovery, therefore suggesting the return or the emergence of some species carrying diversified and/or original traits. This is supported by the partial recovery in CWM trends for traits such as invertebrate-based diet, ground-closer nesters, pursuit/pounce foraging behaviour, and foraging substrates including air and water, together with a halt in the increase of traits associated with forest-dwelling species (Fig. 4). Moreover, we cannot exclude the positive contribution of environmental policies to this recovery, e.g. the Common Agricultural Policy (EU Regulation

1037/2013), which has supported the creation of seminatural features, including woody patches, hedgerows, ponds and fallows. Conversely, the persisting decline of evenness suggests that the return or new acquisition of the previously lost functionalities and originalities can occur more rapidly than, or even without, a recovery of regularity in trait distribution within the functional space. This may be linked to the partially different responses of evenness, compared to richness or divergence, to environmental drivers (e.g. land use) and/or to biotic drivers (e.g. interspecific interactions), which merit specific investigation in future studies.

### Relationships between FD metrics and species richness

The negative relationships between species richness and all the functional diversity metrics (standardised effect size) highlighted that the increase in the number of species in the community reduces the volume of the functional space (i.e. richness) while increasing the similarity and redundancy of traits (decrease in divergence and evenness). Recently, in French vineyards, Bouvier et al. (2024) found a negative association between species richness and functional diversity in avian assemblages. Similarly, our results corroborated such previous findings. This indicates that, in the lowland agricultural landscapes under study, avian assemblages with higher species richness are also less functionally diversified. This pattern is consistent with niche packing, characterised by a denser occupation of the functional space. In environments subject to more stringent ecological filters, which prevent the persistence of species with diversified traits, the coexistence and temporal increase of functionally redundant species may be facilitated by weak interspecific competition among species sharing adaptive traits, provided that resources are not limiting. Consequently, one can observe an increase in species counts while filtering for similar trait values, resulting in higher species richness but a restricted occupied functional space. Additionally, dominance by a pool of numerically abundant species with similar traits can raise species richness locally while reducing abundance-weighted functional diversity metrics. Nevertheless, competitive exclusion may also lead to the filtering out of species with less well-adapted traits at the boundaries of the functional space. However, caution is needed when relating trait space, and the associated functional diversity, to niche space and differentiation (Pigot et al. 2016, Blonder 2018). Contrary to our initial prediction, this negative relationship between functional diversity metrics (SES) and species richness is ecologically important because it highlights that functional facets can negatively covary with species richness, indicating functional loss and redundancy, with direct implications for ecosystem functioning and conservation priorities.

### Functional clustering

In all functional diversity metrics, a widespread presence of functional clustering was found. Functional clustering, also referred as trait underdispersion, occurs when the diversity of the functional space of the observed assemblage is lower than

expected by chance (Kraft et al. 2015, Mammola et al. 2024). In our data, for all FD metrics, functional clustering occurred in more than the half of each distinct site at least once. Temporal trends in functional clustering for all FD metrics were consistent with the trends observed in SESs, resulting in more redundant and clustered communities. Redundancy can be seen as a characteristic that enhances the resilience of a community: being functionally similar, the loss of a species will not result in a loss of functionalities because another species with similar features is present in the assemblage. However, redundant communities, when associated with a reduced volume of the functional space (i.e. lower functional richness than expected by chance), as in our case, indicates that the communities, albeit resilient, performed a reduced set of functionalities. This may be a signal of altered or disturbed environments where a smaller number of functionally similar species can persist under directional environmental pressures. Indeed, functional clustering is often interpreted as being consistent with environmental filtering (Flynn et al. 2009), namely the phenomenon wherein only a specific set of traits can persist under directional environmental constraints (Kraft et al. 2015). In our study, environmental filtering may have arisen because of a reduction in habitat amount, a decrease in habitat quality, or habitat oversimplification. The depletion of agricultural land in favour of built-up areas occurred in the study area may have contributed to a loss of habitat amount as well as to a decrease in suitability for species carrying traits that were beneficial to functional diversity. Indeed, land-use change can be an important driver of functional diversity (Etard et al. 2022), as we found evidence of its effects on both SESs and functional clustering. However, caution is needed, particularly in correlational and observational studies, due to the difficulty of disentangling the effects of interspecific interactions, such as competitive exclusion arising under limiting resource availability (Kraft et al. 2015).

### Effect of land use on functional diversity and clustering

We noted land use alone, even when employing a multiple-scale approach, had limited explanatory power in capturing the complexity of functional structure in avian communities (as indicated by the moderate proportion of deviance explained by the models). A similar result was also reported in Morelli (2018). Nevertheless, significant and meaningful ecologically effects were detected. Land-use effects were quite consistent between SESs and the probability of observing functional clustering (Table 1, Supporting information). This is not surprising by considering their relationship (Supporting information). The negative effect of built-up areas across all FD metrics, and their role to promote functional clustering, emphasises the critical impact of urbanisation. Urbanisation can impact functional guilds (Sol et al. 2014, Wenzel et al. 2023) with significant effects on functional diversity at community level (Matuoka et al. 2020, Sol et al. 2020, Marcacci et al. 2021) by increasing loss, fragmentation and degradation of habitats, along with an increase in human disturbances and changes in resource

availability (Tschardt et al. 2008). This stresses the importance to prevent the conversion of agricultural and natural lands into urban areas. Besides confirming the impact of urbanisation, our findings importantly showed that built-up areas might act as environmental filter at smaller scales, while their effect disappeared at the landscape scale (2000-m). This may suggest that local conditions, if suitable, may compensate increasing levels of urban cover in the surrounding landscape.

The percentage cover of arable land positively affected functional richness (without a reduction in clustering), divergence and evenness (SEs), although these effects were less pronounced in terms of magnitude and at times asymptotic (Supporting information). Although arable land in the study area is predominantly under intensive regimes (9.26 tonnes ha<sup>-1</sup> of maize and autumn-sown grains between 2006 and 2022, source ISTAT [Istituto Nazionale di Statistica] at <http://dati.istat.it>, accessed on 10 February 2024), whose impacts on bird population trends and distributions are well documented (Rigal et al. 2023, Chamizo et al. 2025), assemblages as a whole may respond differently compared to individual species or functional groups (Landázuri et al. 2024). Within the study sites, arable land exhibits the highest percentage cover (100-m buffer: IQR = 24–96%; 500-m buffer: IQR = 33–85%; 2000-m buffer: IQR = 31–77%), and preventing its erosion is important to provide habitats capable of supporting more functionally diverse and less redundant communities. Moreover, the effects of arable land may be modulated by its management regimes (Guerrero et al. 2024); thus, it is important to assess this aspect in future research, particularly given its dominance in this type of landscapes.

Concerning meadows (mainly hayfields in the study area), the positive contribution to functional divergence at local (100-m) and intermediate (500-m) scales highlighted the importance of this type of cultivation in lowlands to promote trait dispersion. These cultivations usually exhibit greater heterogeneity than monoculture, they can supply diversified sources of food (seeds, invertebrates, vertebrates) and support different foraging behaviours, potentially promoting the coexistence of species with more diversified traits (Tamburini et al. 2022). However, in the case of evenness, the increase of meadows' cover led to an increase of clustering. This means that there is an increase in the probability to observe a more redundant community with species occupying similar region of the functional space. Interestingly, this effect was not coupled with a decrease in richness or divergence (instead we found a reduction of clustering in both richness and divergence at the local scale), suggesting that diversification and originality of functional space is maintained.

While orchard cover did not show any effect on functional clustering, it was associated with reduced functional richness at the local (100-m) and intermediate (500-m) scales, alongside increased functional evenness at the landscape scale (2000-m). This pattern may reflect the effects of intensive orchard management, which can lower avian taxonomic diversity and abundances of functional groups (Morgado et al. 2020, Rime et al. 2020), with also implications on functional

diversity (Bouvier et al. 2024). Shrub cover showed opposite effects between the local scale (100-m) and the landscape scale (2000-m), favouring functional diversity and a reduction of clustering at the former scale, and a reversed effect at the latter (for richness and divergence). Shrubs scattered in lowland agricultural landscapes can offer crucial refuges for birds inhabiting shrub layers or edge environments, providing protection from predators and supplying food sources such as berries and insects, as well as nesting sites (Perkins et al. 2000). The switch in effect with increasing shrub cover at larger scales may suggest that, when shrubs become a considerable feature of the agricultural landscape in lowlands, community's traits are more filtered and redundant. This may be linked to the potential negative effects of shrubs at a broader spatial level on typical farmland and grassland communities, along with the positive effect on forest-dwelling birds (Bani et al. 2019, Anderle et al. 2023), without a functional compensation for the lost traits. Differently from shrubs, forest cover showed a positive effect on all the FD at the landscape scale, consistent with its influence in reducing clustering. It is interesting as such effect was not detected at smaller scales; this suggests that residual forest and wooded areas scattered in the agricultural fabric have a positive influence on functional diversity of the studied bird communities when considering the whole landscape context. In agricultural landscapes, forested areas can enhance the landscape heterogeneity, providing habitats that can host species with more diversified traits, such as forest-dwelling species (e.g. Picidae, Paridae) or species associated with trees for nesting or roosting (e.g. Ardeidae, Accipitridae, Columbidae) (Dondina et al. 2022). The same consideration can be done for hedgerows. Hedgerows provide nesting, roosting and foraging sites, provide cover for local movement and may also facilitate movement through landscapes (Hinsley and Bellamy 2000). Indeed, our findings highlighted a similar effect on functional richness and divergence between hedgerows' density (km km<sup>-2</sup>) and forest cover. Seminal habitats, such as forest patches and hedgerows, have proven to have benefit on avian breeder functional groups and taxonomic richness in agricultural landscapes (Frank et al. 2024), and their role to sustain biodiversity is critical at landscape scale (Tschardt et al. 2021). These findings align with land-sharing conservation strategies, where semi-natural elements embedded within agricultural matrices can enhance biodiversity (Gilroy et al. 2014). Surprisingly, the effect of the hedgerows' density (km km<sup>-2</sup>) was negative for the functional evenness at intermediate (500-m) and landscape (2000-m) scales. In a landscape context, hedgerows may have a negative influence on some bird species typical of open farmland (e.g. the northern lapwing *Vanellus vanellus* and the Eurasian skylark). It is possible that a landscape highly interspersed with hedgerows may lead to a lower regularity in the functional space with an increase of the abundance of redundant species while the overall functionalities and originality are not lost (i.e. richness and divergence). An important consideration merits timber plantations. In our study area, they are mostly constituted by poplar plantations (*Populus* spp.). In agricultural context, this type of cultivation

may serve as a surrogate of forest or woodlands, supporting species associated with these habitats (Chiatante et al. 2021, Porro et al. 2021). Notably, we observed their positive influence on all the FD metrics across all spatial scales, suggesting that they can effectively represent a measure to promote a more diversified functional space in avian communities inhabiting agricultural lands. Our findings also stressed the importance of water bodies (both natural and artificial, e.g. streams, lakes, ponds) and wetlands (e.g. marshes) to increase both the functional richness and divergence across all scales and reduce their clustering at the landscape scale. We would like to emphasize that our species pool did not include water birds intrinsically linked to aquatic environments, thereby further highlighting the critical importance of water bodies and wetlands in agricultural contexts. These features are key elements of the agricultural landscape and enhance the landscape's heterogeneity. They can provide essential habitats for nesting and resting and serve as crucial foraging sites for a diverse range of avian species (Davies et al. 2016), with also positive effects on bird communities (Anderle et al. 2022, Zamora-Marín et al. 2024).

It is also important to consider how scale-dependent land-use effects may be linked to ecological factors such as territory size, movement, dispersal and exploitation of resources (Meichtry-Stier et al. 2018, Zellweger-Fischer et al. 2018, Bosco et al. 2024). For example, woody features – whose effects were predominantly detected at larger scales in this study – may strongly influence species with larger territory sizes or contribute to increase landscape heterogeneity. Meadows and shrubs may act locally by enhancing habitat quality, particularly for species with smaller territories or limited foraging ranges.

Finally, to improve the predictability of responses, we recommend that future studies incorporate not only land use but also fine-grain habitat structure, management intensity, and landscape configuration, as these factors can directly influence avian functional structure in agricultural landscapes (Barbaro et al. 2017, Tarjuelo et al. 2021, Guerrero et al. 2024).

## Conclusions

This study sheds light on functional diversity in avian communities within lowland agricultural landscapes. It focused on a quantitative assessment of functional clustering/overdispersion, long-term trends in functional diversity metrics, their relationships with species richness, changes in functional composition, and the effects of land use on functional diversity at multiple spatial scales. We showed that temporal trends in the three essential functional diversity metrics, namely richness, divergence, and evenness, are decoupled from the trend in species richness. Specifically, there was a decline in functional diversity metrics (with a recovery for richness and divergence) and an increase in species richness. These findings, along with evidence of the persistence of functional clustering over time, i.e. trait underdispersion, highlighted

an increase in redundancy, a loss of originality and functional roles, with a shift towards pool of species characterised by omnivorous diet, larger body size, or better adaptation to structurally complex vegetation. We showed that land use can affect functional diversity at multiple spatial scales and is able to be a driver to determine clustering in the functional space, likely acting as environmental filter. Notably, we remarked a detrimental effect of built-up areas on all the functional diversity metrics at local and intermediate scales, as well as the importance of preserving arable land from urbanisation. Meadows and shrubs were important to sustain functional diversity at the local scale, particularly enhancing functional divergence. Woody features, such as timber plantations, hedgerows, and forest patches, increased functional diversity primarily at the landscape scale. Interestingly, the effect of hedgerows was reversed for functional evenness; water bodies and wetlands increased functional richness and divergence but had no detectable effect on evenness. From a management perspective, this suggests encouraging woody features at the landscape level, promoting cultivation heterogeneity and shrubs locally, preserving or restoring wetlands, and avoiding overly complex vegetation structure in landscapes that are already structurally closed.

Multi-scale planning should be considered in agri-environmental schemes as differential responses may arise in relation to the spatial level of analysis. The integration of multiple diversity metrics along with an accurate assessment of clustering or overdispersion in the functional space can contribute to a deeper understanding of processes that shaped community functional structure over space and time.

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## Author contributions

**Pietro Tirozzi:** Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Investigation (supporting); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Olivia Dondina:** Methodology (supporting); Supervision (equal); Writing – review and editing (equal). **Valerio Orioli:** Data curation (lead); Investigation (lead);

Methodology (supporting); Writing – review and editing (equal). **Luciano Bani**: Data curation (lead); Investigation (lead); Project administration (lead); Supervision (equal); Writing – review and editing (equal).

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bzkh189r4> (Tirozzi et al. 2025).

### Supporting information

The Supporting information associated with this article is available with the online version.

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