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RESEARCH ARTICLE

Agricultural intensification degrades arable weed diversity into phylogenetically unstructured subsets of tolerant species

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Abstract

Context The rise of agricultural intensification (AgI) has severely impacted arable weeds, making it crucial to understand how this process shapes their assemblages across agricultural landscapes.

Objectives To elucidate how variation in species composition (beta diversity) among arable weed assemblages respond to AgI gradients, with a particular focus on whether phylogenetic relationships structure these patterns.

Methods We analyzed farm-level arable weed assemblages across nine European regions with distinct agricultural management contexts, focusing on in-field AgI indicators (yield, nitrogen fertilizer, pesticides) and landscape context (field size, cultivated area, crop diversity). To examine compositional changes among assemblages, we partitioned beta diversity into its turnover and nestedness components.

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Results We found positive correlations between in-field AgI differences among farms and the nestedness component of taxonomic beta diversity, alongside a previously reported negative relationship between in-field AgI and species richness. In contrast, the landscape dimension of AgI had a comparatively minor effect. Phylogenetic structure metrics showed weak and inconsistent responses to AgI.

Conclusions In-field variation in AgI—rather than landscape context—contributes significantly to taxonomic dissimilarity among arable weed assemblages on European farms, with increasing AgI driving the exclusion of sensitive species and the persistence of tolerant ones, without evidence of species potentially restricted to highly intensified conditions. Traits associated with AgI likely evolved through distinct and complex evolutionary trajectories long before the surge of AgI in the mid-twentieth century, which may explain the phylogenetically unstructured patterns observed.

Keywords Agricultural intensification · Arable weeds · Compositional dissimilarity · European farms · Phylogenetic dissimilarity · Phylogenetic divergence · Species richness

Introduction

Agriculture is the most widespread land use in Europe, covering approximately 40% of its total land area (Eurostat 2020). As a result, European farmlands harbour a significant share of the biological diversity of the continent (Emmerson et al. 2016). However, the rise of agricultural intensification (AgI) since the mid-twentieth century has severely impacted agricultural biodiversity (Chamberlain et al. 2000; Tilman et al. 2001; Green et al. 2005), with arable weeds being particularly affected (Guerrero et al. 2010; Carmona et al. 2020). These plants are the foundation of trophic and mutualistic networks that shape the diversity and composition of agricultural ecosystems (Butler et al. 2010; Eraud et al. 2015; Evans et al. 2011; Gay et al. 2024), and underpin essential ecosystem services such as biological pest control and pollination (Scherber et al. 2010; Brooks et al. 2012; Ebeling et al. 2012; Bretagnolle & Gaba 2015; Gaba et al. 2020). Consequently, any disruption to these plants may have far-reaching consequences for human well-being.

The negative impact of AgI on the diversity of arable weeds is twofold, reducing species richness (Geiger et al. 2010; Guerrero et al. 2010) and diminishing functional diversity (Guerrero et al. 2014), a pattern that appears consistent across many European countries and agricultural contexts (Billeter et al. 2008; Storkey et al. 2012; Carmona et al. 2020). This is partly driven by the decline of species adapted to local conditions within increasingly rare crops, such as flax (*Linum usitatissimum* L.), and of species suited to nutrient-poor habitats, which are shrinking due to the increased use of fertilizers (Storkey et al. 2012). However, despite extensive research on the impacts of AgI on arable weeds, important gaps remain in understanding how species composition varies among assemblages in response to AgI, particularly in relation to the turnover and nestedness components of beta diversity, which may reveal overlooked patterns of community assembly (Baselga et al. 2010).

As AgI reduces the diversity of arable weeds (Guerrero et al. 2010), the resulting impoverished assemblages may be dominated by species that can persist across a broad range of AgI levels (referred to as 'tolerant' hereafter). This scenario would lead to taxonomic nestedness, where impoverished assemblages under high AgI conditions are subsets of those under low AgI (Fig. 1). Alternatively, high AgI conditions may lead to both reduced species richness and a compositional shift toward species potentially adapted to high nutrient inputs and regular agrochemical use. These species (referred to as 'high-AgI specialists' hereafter) might, however, be poorly suited to less intensified systems, where they would be easily outcompeted by slower-growing species adapted to milder management regimes (Grime 1977). If a trade-off exists between adaptation to high- and low-AgI conditions, it would lead to taxonomic turnover along the AgI gradient (Fig. 1). Thus, whether AgI consistently promotes taxonomic nestedness or turnover remains largely unknown. Furthermore, it remains unclear whether phylogenetic relationships influence the response of arable weed assemblages to AgI. For example, if traits conferring suitability to AgI (e.g., tolerance to agrochemicals, efficient nutrient-uptake

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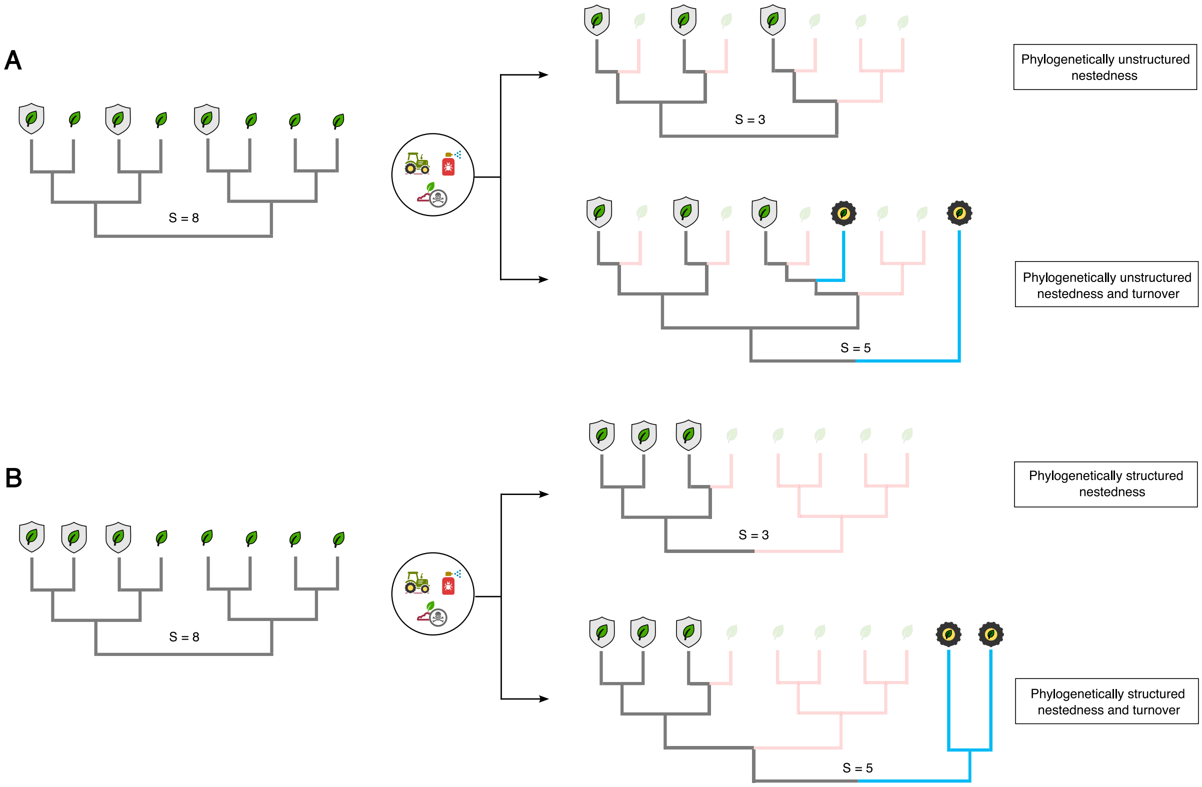

Fig. 1 Compositional changes between hypothetical arable weed assemblages following agricultural intensification (AgI). (**A**) After AgI impacts the assemblages, species richness declines as species unable to tolerate intensified conditions are excluded. AgI-tolerant species (represented by a shield symbol) persist, resulting in assemblages that are partially or entirely nested within those present prior to AgI. However, the colonization of potential high-AgI specialists—species represented by a tractor wheel that would not thrive under pre-AgI conditions—introduces species turnover. Since neither AgI-tolerant species nor high-AgI specialists are phylogenetically clustered, these compositional changes (via nestedness or turnover) are not phylogenetically structured. (**B**) Same scenario as in (**A**), but in this case, compositional changes are phylogenetically structured, suggesting non-random phylogenetic patterns in species loss and gain. Note that phylogenetically structured changes lead to the loss of an entire clade with deep evolutionary roots. All symbols are licensed under Creative Commons CC BY 3.0, credited to visual language (tractor: https://thenounproject.com/icon/tractor-6936508/), Andi wiyanto (shield: https://thenounproject.com/icon/shield-4879405/), BnB Studio (leaf: https://thenounproject.com/icon/leaf-7836470/), ahmadwil (skull: https://thenounproject.com/icon/skull-7667371/), Creative Mahira (herbicides: https://thenounproject.com/icon/herbicides-7107323/), and Adrien Coquet (pesticides: https://thenounproject.com/icon/pesticide-5454777/)

strategies) are phylogenetically conserved, the loss of AgI-sensitive species would lead to more clustered assemblages (Fig. 1). This would result in a disproportionate loss of phylogenetic—and potentially functional—diversity, with important implications for ecosystem functioning (Flynn et al. 2011) and stability (Cadotte et al. 2012). Thus, identifying whether certain clades are disproportionately vulnerable to AgI can inform more strategic conservation efforts aimed at preserving not only species, but also the evolutionary history they represent and the associated benefits (Molina-Venegas et al. 2021). In this context, Egorov et al. (2014) found no consistent relationship between the phylogenetic divergence of plants in grasslands, as measured by the Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD), and land-use intensification in Germany. These authors suggested that the absence of phylogenetic signal in land-use sensitive traits could explain their findings. However, since their study focused on plants associated with grasslands rather than cropfields (i.e., arable weeds), their results are difficult to extrapolate to arable weed assemblages.

AgI can influence species diversity through different pathways. On the one hand, mechanisms that alter species' performance at the (local) field scale (hereafter referred to as 'in-field AgI') include nitrogen inputs, which favours resource-acquisitive species (Wang et al. 2022); herbicide applications, which can effectively eradicate locally rare plant species (Gaba et al. 2016); and insecticides, which disrupt plant–herbivore trophic interactions (Haag et al. 2004) and plant-pollinator networks (Brittain and Potts 2011). On the other hand, changes in landscape configuration (hereafter referred to as 'landscape AgI') can alter meta-community dynamics, thereby impacting species diversity (Roschewitz et al. 2005). For example, the shrinking of natural habitats caused by the expansion of crop-field sizes and increased area of cultivated land may hinder the effective dispersal of arable weeds from source to sink populations (Bourgeois et al. 2020). Additionally, the simplification of habitat structure in intensified monoculture landscapes is expected to lower the richness of arable weeds compared to landscapes characterized by a high diversity of crop types, as the latter provide greater crop-related habitat heterogeneity for arable weeds. Therefore, it is crucial to consider both the in-field and landscape dimensions of AgI when evaluating its effects on the taxonomic and phylogenetic diversity of arable weed assemblages.

Here, we examine how variation in species composition (beta diversity) among arable weed assemblages respond to in-field and landscape AgI gradients in nine European regions encompassing different biogeographical and management contexts. More specifically, we address the following questions: (i) What mechanism related to beta diversity underlies compositional changes in response to in-field and landscape AgI: the replacement of AgI-sensitive species by potential 'high-AgI specialists' (i.e. turnover), or the loss of AgI-sensitive species alongside the persistence of tolerant species (i.e. nestedness, sensu Balselga, 2010)? and (ii) Are phylogenetic relationships of species related to the diversity patterns observed in (i)? Although previous studies have examined how AgI affects species richness (i.e., taxonomic alpha diversity) across European farms (Carmona et al. 2020), phylogenetic divergence (i.e., phylogenetic alpha diversity) has received little attention. Since alpha diversity is instrumental in informing beta diversity patterns, we also (iii) assessed the relationship between AgI and both species richness and phylogenetic divergence to gain a more comprehensive understanding of how variation in species composition among arable weed assemblages responds to AgI.

Materials and methods

Study design and sampling procedure

Data collection took place on cereal-producing farms across nine European regions, located in Spain, France, Ireland, Germany (with both western and eastern regions), The Netherlands, Poland, Estonia and Sweden (Fig S1). These regions span a broad geographic and climatic range, resulting in distinct agricultural management contexts summarized in Emmerson et al. (2016). In each region, between 15 and 30 farms (units of analysis) were selected according to a gradient of regional agricultural intensification (AgI), each located at least 1 km apart. To minimize variation in species pool size and compositional dissimilarity within regions, and to avoid excessive landscape heterogeneity and soil differences, farms were distributed across total areas ranging from 30×30 km^2 to 50×50 km^2 within each region. These farms served as analytical units of the study, encompassing a broad spectrum of agricultural management practices. Each farm consisted of one or more winter wheat fields, no more than 1 km apart, all managed by the same farmer (whether owned or leased), covering a total area of up to 1 km^2. Farms were selected to maximize the range of winter wheat yield within each region, based on data from the previous three years as reported by the farmers.

Sampling took place between June and July 2007, and it was synchronized across regions based on the phenology of winter wheat, specifically during the flowering to milk-ripening period. To minimize phenological differences among samples, the order of farm sampling was randomized within each region. At each farm, we selected five sampling points that were distributed over a maximum of five winter wheat fields, with winter barley fields sampled as substitutes when wheat was unavailable (20% of cases). Only non-irrigated fields exceeding 1 hectare were included. If a farm had fewer than five fields, sampling points were allocated proportionally to field size. Sampling points were positioned 10 m from and parallel to grassy, non-woody field borders. At each point, weeds were surveyed within three 2 × 2 m plots arranged in a row, spaced 5 m apart (see Emmerson et al. 2016). A total of 1075 sampling points were surveyed across all farms.

All angiosperm plants, except for crops, were identified to the species level in each plot. Data from the three plots at each sampling point were pooled to calculate the frequency of occurrence of each species, which served as a proxy for their abundance at the field level, ranging from 0 (absent) to 3 (present in the three plots). These values were then averaged across all sampling points within each farm to estimate the abundance of each species at the farm level, and all subsequent analyses were based on this farm-level data.

Agricultural intensification information

We used eight indicators of in-field and landscape AgI. For in-field AgI, data were collected through questionnaires completed by the farmers managing the sampled fields. These indicators included yield, inputs of nitrogen fertilizer, herbicides, and insecticides (Table 1). For landscape AgI, indicators were derived from digital maps based on remotely sensed images. These included field size, proportion of cultivated area, and crop diversity. Field sizes were directly extracted from the digital maps, while the proportion of cultivated area and crop diversity were estimated using circular plots with a 500-m radius centred on each sampling point. All indicators were recorded for each sampled field and averaged at the farm level (Emmerson et al. 2016). We derived an integrated index of AgI for each farm k and dimension of AgI:

$$AgI_k = \frac{\sum_{i=1}^{n} (y_{ik} - y_{i.min}) / (y_{i.max} - y_{i.min})}{n} \tag{1}$$

where y_{ik} is the observed value of indicator i in farm k, $y_{\mathrm{i.min}}$ and $y_{\mathrm{i.max}}$ are the minimum and maximum observed values for indicator i across all farms, respectively, and n is the total number of indicators for each dimension of AgI (Flohre et al. 2011). Higher values of the indicators reflect greater AgI, except for crop diversity, since a higher diversity of crop types promotes greater crop-related habitat heterogeneity for arable weeds. To ensure consistency in the directionality of all indicators, crop diversity was inverted [using $1—(y_{ik} - y_{i.min})$ in Eq. 1], ensuring its maximum value was reached in monoculture farms. The correlation between the in-field and landscape AgI indices was very weak ($R^2 = 0.04$), suggesting no collinearity issues between these variables (see Fig. S2 for correlations between each AgI index and its corresponding individual indicators, as well as correlations among the individual indicators themselves).

Taxonomic harmonisation and phylogenetic trees

We used the 'randtip' R package (Ramos-Gutiérrez et al. 2023) to construct a comprehensive phylogeny of all arable angiosperm weeds observed across the farms (n = 390), building upon the most comprehensive molecular and time-calibrated backbone tree of plants available to date (Jin and Quian, 2022 based on Smith & Brown 2018, megatree). Prior to this, we harmonized the botanical nomenclature in our

Table 1 Agricultural management indicators for the in-field and landscape dimensions of intensification

Dimension	Indicator	Description
In-field	Yield	Amount of winter wheat grain produced by field annually (kg/ha)
	Nitrogen fertilizer	Amount of active ingredient of nitrogen fertilizer applied to field over the agricultural year (kg/ha)
	Nº herbicide applications	Number of times herbicide is applied to field over the agricultural year
	Amount of herbicide	Amount of active ingredient of herbicide applied to field over the agricultural year (kg/ha)
	Nº insecticide applications	Number of times insecticide is applied to field over the agricultural year
Landscape	Field size	Extent of sampled field (ha)
	% cultivated area	Percentage area of arable crops within a 500 m radius circle centred on sampled field
	Nº crops	Number of different crop types within a 500 m radius circle centred on sampled field

dataset using the WorldFlora R package (Kindt 2020). The process revealed 112 phylogenetically uncertain taxa (PUTs), that is, species missing in the backbone phylogeny or that could not be identified at the species or genus level. These taxa were subsequently incorporated through a systematic procedure based on taxonomic ranks (Ramos-Gutiérrez et al. 2023). Each PUT was bound to a randomly chosen branch below the node representing the most recent common ancestor (MRCA) of its congeneric species. From now on, these species will be referred to as phylogenetically placed and co-ranked (PPCR) species, as will any group of species sharing a taxonomic rank with a PUT in the backbone tree. The probability of selecting a branch was proportional to its length, with the insertion point randomly chosen from a uniform distribution. In cases where no congeneric PPCR species were identified, the PUTs were attached below the MRCA of their PPCR species in the next available taxonomic rank (consubtribals, contribals, consubfamiliars, and confamiliars), ensuring the monophyly of the groups contained within the MRCAs was maintained. PUTs associated with singleton clades (i.e. PPCR species represented by one single terminal branch) were bound to a randomly selected point along the corresponding phylogenetic tip. When PPCR species formed paraphyletic groups, the PUTs were bound below the MRCA of all PPCR species, excluding the diverging clade to avoid creating a polyphyletic group during the binding process. In cases where PPCR species formed polyphyletic groups, we considered various binding approaches, customized to the specifics of each situation to prevent suboptimal outcomes (see Ramos-Gutiérrez et al. 2023). In most cases, the PUTs were placed within the largest monophyletic group of PPCR species, assuming a higher probability of mapping within this group. In situations where the largest group was not decisively larger than the second largest group of PPCR species (thus providing less conclusive evidence that the former includes the PUT) and no clear outliers were present, we used a probabilistic approach to randomly select a cluster for insertion, with the probability of selection being proportional to the size of the cluster ('frequentist' scheme, see Ramos-Gutiérrez et al. 2023). In a few instances where major monophyletic clusters were not apparent and outliers were present, we manually defined the clades for PUT insertion to include the majority of PPCR species while excluding outliers. In the two cases where a few 'intruders' were detected within the cluster of PPCR species, we bound the PUTs below the MRCA of all their PPCR species ('complete' scheme) (see Table S1 for details on the binding parameters set for each PUT). Finally, the hybrid species *Alopecurus myosuroides x pratensis* was assigned to either of its parental species (*Alopecurus myosuroides* or *Alopecurus pratensis*) with equal probability. After binding all the PUTs to the backbone tree, we pruned it to retain only the species in our dataset. To account for phylogenetic uncertainty in the analysis, we repeated the procedure to generate 100 trees, and the results were averaged across all trees.

Phylogenetic divergence

We computed the phylogenetic divergence of the arable weed assemblage on each farm using the abundance-weighted Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD) metrics. MPD is the abundance-weighted average distance among all possible taxa pairs in an analytical unit (a farm), while MNTD measures the abundance-weighted average distance from each taxon to its closest relative in the analytical unit (Webb et al. 2002). The two metrics are complementary because MPD is highly sensitive to 'deep' branching structure, while MNTD describes the more 'terminal' dimension of phylogenetic divergence (Mazel et al. 2016). To account for the effect of species richness on phylogenetic divergence, we computed a standardized effect size (SES) score for each farm and metric as:

$$SES = \frac{Obs - Mean_{null}}{SD_{null}} \tag{2}$$

where 'Obs' is the observed value of the metric, and '$\mathrm{Mean}_{\mathrm{null}}$' and '$\mathrm{SD}_{\mathrm{null}}$' are the mean and standard deviation of a null distribution of values obtained by shuffling taxa labels in the phylogenetic distance matrix 999 times. Higher SES scores indicate greater phylogenetic divergence compared to random expectation. In contrast, lower SES scores suggest reduced phylogenetic divergence (increased phylogenetic clustering) relative to random expectation. SES scores were computed with the 'Picante' R package (Kembel et al. 2010), and phylogenetic distances were obtained from each tree using the *cophenetic* function (R Core Team 2023).

Statistical modelling

We assessed the impact of AgI on the richness of arable weeds by fitting a generalized linear mixed-effects model with a Poisson error distribution and a log link function. The model included both in-field and landscape AgI indices as fixed-effect predictors, with species richness per farm as the response variable. To account for variation in species richness across countries, we incorporated a random intercept for each region while keeping slopes fixed. All explanatory variables were standardized to have a mean of zero and unit variance to enhance model convergence and interpretability. The model was fitted using the *glmer* function from the ‘lme4’ R package (Bates et al. 2015). The proportion of variance jointly explained by the fixed-effect predictors (i.e., Nakagawa’s marginal R^2; Nakagawa et al. 2013), along with partial R^2 values for each predictor, was estimated using the *partR2* function from the ‘partR2’ R package (Stoffel et al. 2021), with 1000 parametric bootstrap iterations to obtain 95% confidence intervals. A similar modelling approach was employed to evaluate the impact of AgI on the ‘deep’ and ‘shallow’ phylogenetic divergence of arable weed assemblages. Separate mixed-effects models were fitted for each response variable—SES.MPD (deep divergence) and SES.MNTD (shallow divergence)—assuming Gaussian error distributions. These models were fitted using the *lmer* function from the ‘lmerTest’ R package (Kuznetsova et al. 2017).

Variation in species and lineage composition with agricultural intensification

We first quantified taxonomic pairwise beta diversity among the farms in each region to determine whether AgI influenced variation in species composition. Taxonomic beta diversity was calculated with the *beta.pair* function from the ‘betapart’ R package (Baselga et al. 2012), using the Sorensen pairwise dissimilarity index ($\beta_{sor} = 1$—Sorensen). $\beta_{sor} = 0$ indicates identical species composition between the two farms being compared, while $\beta_{sor} = 1$ indicates that no species are shared (maximum taxonomic dissimilarity). Additionally, we examined the two additive components of Sorensen dissimilarity, namely turnover (β_{sim}) and nestedness (β_{nes}). β_{sim} refers to the replacement of some species by others between the farms, while β_{nes} captures the dissimilarity in species composition that arises from differences in species richness—i.e., without any species replacement (Baselga 2010). Next, we conducted six Mantel tests per region, relating each component of beta diversity (β_{sim}, β_{nes}, and the total, β_{sor}) to the Euclidean distances among the values of the in-field and landscape AgI index, respectively. Statistical significance was assessed using 999 permutations of the corresponding beta diversity matrix for each comparison.

We also quantified phylogenetic pairwise beta diversity among farms in each region using the Phylosor pairwise dissimilarity index ($\beta_{phy\text{-}sor} = 1$—Phylosor). $\beta_{phy\text{-}sor}$ measures the proportion of phylogenetic branches subtending the species in two farms that are not shared between them. Thus, $\beta_{phy\text{-}sor} = 0$ indicates that all phylogenetic branches are shared between the farms, while $\beta_{phy\text{-}sor} = 1$ signifies that no branches are shared (maximum phylogenetic dissimilarity). Additionally, we examined the two additive components of $\beta_{phy\text{-}sor}$, namely phylogenetic turnover ($\beta_{phylo\text{-}sim}$) and nestedness ($\beta_{phylo\text{-}nes}$). $\beta_{phylo\text{-}sim}$ refers to the replacement of some lineages by others between two farms, while $\beta_{phylo\text{-}nes}$ captures dissimilarity in lineage composition that arises from differences in phylogenetic diversity between the farms—i.e., without any lineage replacement (Leprieur et al. 2012). Taxonomic and phylogenetic beta diversity metrics are highly correlated (Table S2), hence we standardized the latter ($\beta_{phylo\text{-}sim}$, $\beta_{phylo\text{-}nes}$, and their additive effect, $\beta_{phylo\text{-}sor}$) using Eq. (2). This standardization, based on null models generated by randomizing taxa labels within each region (999 iterations), accounts for species compositional differences that drive the correlation, thereby isolating phylogenetic beta diversity patterns beyond taxonomic beta diversity alone. As a result, higher SES scores indicate greater phylogenetic beta diversity than expected based on the pattern of species overlap between pairs of farms, while lower SES scores suggest less phylogenetic beta diversity than expected. We conducted six Mantel tests per region, relating each component of standardized phylogenetic beta diversity (SES.$\beta_{phylo\text{-}sim}$, SES.$\beta_{phylo\text{-}nes}$, and SES.$\beta_{phy\text{-}sor}$) to the Euclidean distances among the values of the in-field and landscape AgI index, respectively. Statistical significance was assessed using 999 permutations of the corresponding phylogenetic beta diversity matrix for each comparison.

Results

Species richness and compositional dissimilarity

We found a strong negative relationship between agricultural intensification (AgI) and species richness (marginal $R^2 = 0.276$, 95% CI 0.176, 0.421). While both in-field and landscape AgI exerted significant effects, in-field AgI was a much stronger predictor of species richness than landscape AgI (Fig. 2).

The beta diversity analysis revealed that total dissimilarity in species composition (β_{sor}) among farms within each region was generally moderate to high, exceeding 50% in most cases (Table S3). Taxonomic turnover (β_{sim}) was predominantly higher than nestedness (β_{nes}), indicating that variation in species composition is primarily driven by the actual replacement of species rather than by differences in species richness between farms. However, in-field AgI differences were positively and significantly correlated with β_{nes} in five out of nine regions, whereas no significant correlations were found with β_{sim} (Table 2). Further, we found a strong positive correlation between (i) the Pearson *r* values for the relationship between in-field AgI and β_{nes} and (ii) the standard deviation of in-field AgI values (adjusted $R^2 = 0.54$; estimate = 0.029; p-value = 0.014). This suggests that the relationship between in-field AgI and β_{nes} is more pronounced in countries with higher variability in in-field AgI. Finally, landscape AgI was correlated with β_{nes} in only one region (Table 2).

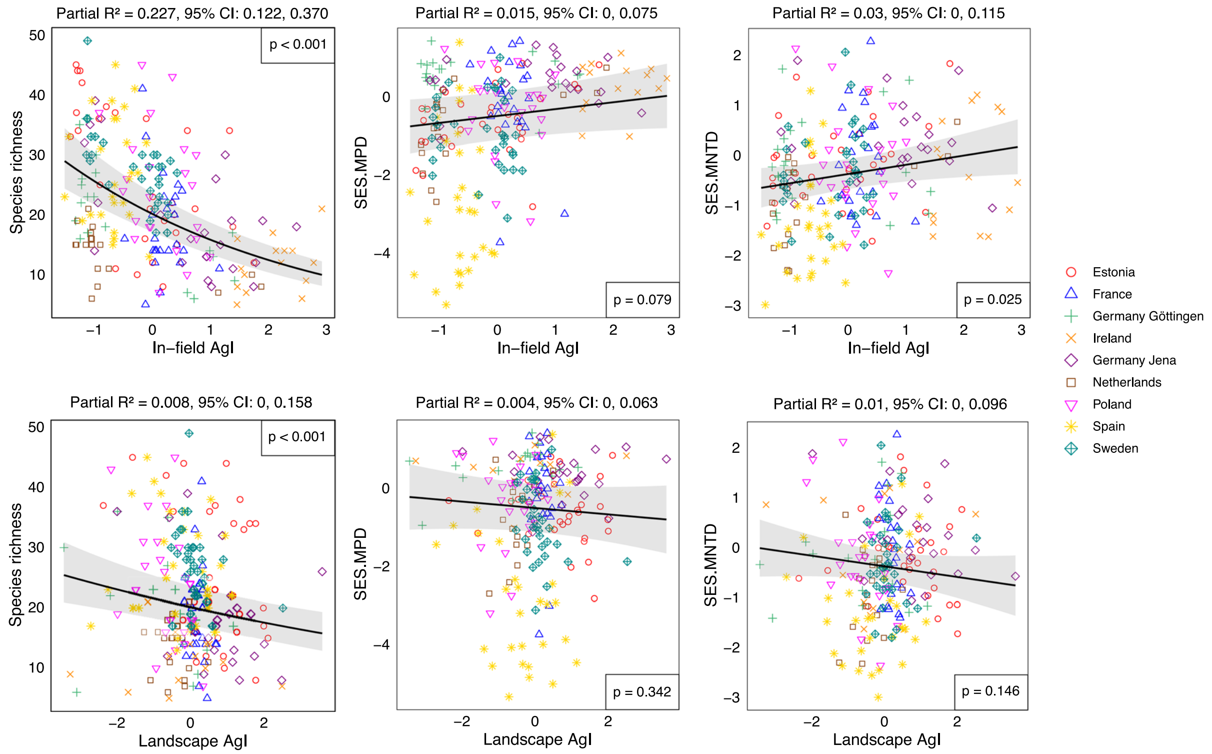

Fig. 2 Scatter plots illustrating the bivariate relationships between agricultural intensification (AgI) and three metrics of alpha diversity: species richness, 'deep' phylogenetic divergence (SES.MPD), and 'shallow' phylogenetic divergence (SES.MNTD). The top and bottom rows of panels depict partial relationships for the in-field and landscape dimensions of AgI, respectively, after accounting for variation attributable to country as a random effect. The trend lines represent predictions with 95% confidence intervals from three models: a generalized linear mixed-effects model with a Poisson error distribution for species richness, and two linear mixed-effects models with Gaussian error distributions for SES.MPD and SES.MNTD

Table 2 Strength (Pearson r), direction (sign), and statistical significance (p-values) of the relationships between (i) taxonomic beta diversity among arable weed assemblages (farm-level) within each region —turnover (β_{sim}), nestedness (β_{nes}), and their additive effect (β_{sor})— and (ii) differences in agricultural intensification (AgI index) among farms, measured through both in-field and landscape indicators. Beta diversity was computed using the 1 – Sørensen dissimilarity index, while Euclidean distance was used to compute differences in AgI

	In-field						Landscape					
	β_{sim}		β_{nes}		β_{sor}		β_{sim}		β_{nes}		β_{sor}	
	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value
Estonia	– 0.045	0.759	**0.215**	**0.007**	**0.275**	**0.001**	– 0.119	0.906	0.062	0.173	– 0.048	0.705
France	0.020	0.479	0.036	0.297	0.070	0.283	0.037	0.383	– 0.067	0.648	– 0.020	0.581
Germany Göttingen	0.055	0.336	**0.461**	**0.002**	**0.473**	**0.002**	– 0.007	0.551	0.135	0.137	0.115	0.251
Germany Jena	– 0.145	0.930	**0.266**	**0.007**	0.087	0.189	– 0.201	0.925	**0.250**	**0.018**	– 0.005	0.490
Ireland	– 0.086	0.798	0.125	0.106	0.012	0.430	0.034	0.412	0.037	0.341	0.074	0.322
Netherlands	0.181	0.131	**0.278**	**0.027**	**0.374**	**0.025**	– 0.036	0.558	– 0.014	0.517	– 0.045	0.553
Poland	– 0.063	0.733	– 0.001	0.496	– 0.080	0.817	0.099	0.193	0.089	0.184	0.216	0.050
Spain	0.010	0.441	– 0.048	0.667	– 0.032	0.638	0.077	0.159	– 0.069	0.789	0.025	0.361
Sweden	– 0.177	0.993	**0.326**	**0.001**	0.101	0.091	0.020	0.430	0.082	0.185	0.110	0.153

Significant relationships at the 5% nominal alpha level are indicated in bold

Phylogenetic divergence and lineage dissimilarity

The relationship between AgI and phylogenetic divergence was very weak for both SES.MPD (marginal $R^2 = 0.016$, 95% CI 0.001, 0.076) and SES.MNTD (marginal $R^2 = 0.035$, 95% CI 0.004, 0.120). Neither in-field nor landscape AgI had a significant effect with the exception of in-field AgI on SES.MNTD, which showed a modest but significant positive association (Fig. 2).

As with β_{sim} and β_{nes}, phylogenetic turnover ($\beta_{phylo\text{-}sim}$) was generally more prominent than phylogenetic nestedness ($\beta_{phylo\text{-}nes}$). However, the contributions of $\beta_{phylo\text{-}sim}$ and $\beta_{phylo\text{-}nes}$ to total phylogenetic dissimilarity ($\beta_{phylo\text{-}sor}$) were more similar to each other than those of β_{sim} and β_{nes} to β_{sor} (Table S3). Additionally, SES.$\beta_{phylo\text{-}nes}$ and SES.$\beta_{phylo\text{-}sim}$ significantly correlated with in-field and landscape AgI differences in only one and two regions, respectively (Table S4).

Discussion

Our findings align with previous studies showing that agricultural intensification (AgI) is a significant driver of the decline in arable weed diversity across various biogeographical and management contexts (Hyvönen et al. 2008; Liira et al. 2008; Guerrero et al. 2010; Storkey et al. 2012; Carmona et al. 2020; Fonderflick et al. 2020). Furthermore, we found that AgI significantly contributes to taxonomic dissimilarity among arable weed assemblages on European farms, with increasing in-field AgI leading to the exclusion of sensitive species and the persistence of tolerant ones, but without evidence of species potentially restricted to highly intensified conditions. These insights enhance our understanding of the processes driving compositional changes in arable weed assemblages under AgI, and can inform targeted management strategies aimed at preserving functional diversity and sustaining ecosystem services within agroecosystems.

The positive correlations between AgI differences among farms and taxonomic nestedness suggest that the decline in arable weed diversity is largely driven by the filtering out of AgI-sensitive species while tolerant species persist. For example, most farms in the Göttingen region of Germany harbour tolerant species such as *Cirsium arvense* (L.) Scop., *Stellaria media* (L.) Vill., and *Tripleurospermum inodorum* (L.) Sch. Bip. These species can thrive in a wide range of AgI conditions due to their high seed bank survival, germination rates, seed production, and tolerance to tillage, traits that enable strong colonization abilities and adaptability to disturbed environments (Fried et al. 2012; McKechnie and Sargent 2013; Gaba et al. 2017). In contrast, *Achillea millefolium* L., a comparatively less competitive species dependent on specific conditions such as soil humidity, was primarily found in species-rich, low-AgI farms, where it may benefit from less intensive agricultural practices. Indeed, many species found in species-rich farms are locally rare, and the increased use of herbicides is known to be highly effective in eradicating these species (Gaba et al. 2016). On the other hand, the lack of correlation between AgI differences and taxonomic turnover—alongside the observed decline in arable weed diversity with increasing AgI—does not support the hypothesis that AgI promotes the establishment of potential high-AgI specialists that would be unsuited to low-intensity systems. Instead, AgI-tolerant species persist across a range of agricultural intensities and contribute to biotic homogenization across agroecosystems (Clavel et al. 2011). This suggests that restoring diverse arable weed communities may require more than simply reducing agricultural intensity; it also involves facilitating the establishment of species adapted to low-intensity systems and managing competition from persistent AgI-tolerant species. Furthermore, more diverse weed communities may reduce the competitive pressure on crops (Storkey and Neve 2018), adding agronomic relevance to the primary environmental goal of restoring arable weed diversity.

Both species richness and compositional variation were more sensitive to in-field than to landscape AgI, suggesting that the primary impacts of AgI on arable weed diversity likely occur through local ecological mechanisms, including altered competitive dynamics that lead to the exclusion of slow-growing species under high fertilizer use (Blackshaw and Brandt 2008; Storkey et al. 2012), or the eradication of herbicide-sensitive plants due to intensified chemical control (Gaba et al. 2016). Supporting this, previous studies have shown that high levels of AgI favour species with traits that enable them to avoid competition with crops—either through early flowering (Guerrero et al. 2014) or by adopting a fast-growing ruderal strategy (Carmona et al. 2020)—or to cope with competition by attaining greater stature to overcome low light availability (Guerrero et al. 2014). Additionally, increasing herbicide pressure has been proposed as an environmental filtering mechanism that can act against early-germinating species unable to avoid early-season herbicide treatments (Fried et al. 2012). On the other hand, also consistent with previous findings (Carmona et al. 2020), landscape-level AgI seems to have a comparatively minor effect on arable weed diversity, at least based on the variables analysed in this study. This is likely due to the high seed persistence, dispersal and colonization ability of these plants, which can use crop edges and roadsides between agricultural fields as ecological refuges and dispersal corridors (Sosnoskie et al. 2007). In contrast, other taxonomic groups that require more connected habitats for feeding and breeding, such as birds and insects, may be more influenced by landscape factors (Guerrero et al. 2010, 2012). Nonetheless, we acknowledge that landscape-level AgI is a complex phenomenon, and thus our composite metric may underestimate its impact on arable weed assemblages, as other potentially relevant variables—such as direct measures of habitat fragmentation—could also be influential (Listl and Reisch 2014). This limitation may reflect the fact that our sampling framework was designed to balance both landscape and in-field AgI gradients, rather than to deliberately maximize variation in landscape complexity. Additionally, our landscape-level indicators may not capture temporal dynamics of intensification, such as interannual variability in the extent and spatial distribution of cultivated area, which may also influence arable weed assemblages (Blank et al. 2023).

The relationship between in-field AgI differences among farms and taxonomic nestedness was most pronounced in regions with high variability in AgI. Regions like Ireland, which exhibit relatively low variability along the in-field AgI gradient, showed no significant relationship, as the uniformly high intensification levels observed there result in all farms being similarly impoverished in arable weeds. Regions with low variability along the in-field AgI gradient but overall low intensities, such as Spain, did not show a significant relationship either, likely because AgI was not high enough to cause a significant loss of AgI-sensitive species. Indeed, a substantial decline in species richness is observed in regions with more pronounced differences along the in-field AgI gradient, such as Estonia and the two German regions.

While AgI was not correlated with the turnover of species among farms, it is worth noting that the latter was the predominant component of assemblage dissimilarity across all regions. Thus, future studies should address the drivers of dissimilarity through species replacement, including variations in microenvironmental conditions among farms, farm-specific agricultural practices (such as crop rotation or irrigation management), and differences in management legacies among farms. Nonetheless, the importance of nestedness patterns among arable weed assemblages has been highlighted in previous work (Carmona et al. 2017), lending further support to the relevance of the relationship between AgI and nestedness-driven taxonomic dissimilarity identified in our continental scale analysis.

Although AgI can be traced back to the Neolithic (Bellwood 2005), its current levels are unprecedented compared to those before the mid-twentieth century, when the Green Revolution took off (Evenson & Gollin 2003). This recent and dramatic increase suggests that the absence of potential high-AgI specialist plants, which would be confined to highly intensified agricultural landscapes, may result from insufficient time for evolutionary processes to keep pace with the rapid changes brought about by the Green Revolution. In addition, the multifaceted nature of AgI suggests that while some associated traits may trace deep evolutionary roots, others may have evolved independently across lineages in response to ecological conditions that long predate the surge of AgI in the past century, which could help explain the lack of a clear relationship between AgI and phylogenetic divergence (Cadotte et al. 2017). Although we found a significant positive effect of in-field AgI on 'shallow' phylogenetic divergence (SES.MNTD), contrasting with our expectation of a negative relationship, we consider the effect too weak to support firm conclusions. Nonetheless, these results do not rule out the potential for ongoing AgI-driven population differentiation within species, whereby populations subjected to higher levels of AgI may experience genetic drift and subsequent shifts in trait values (Kwiecińska-Poppe et al. 2020), or even adaptive genetic changes. For example, certain populations of *Amaranthus palmeri* S. Wats. have developed glyphosate resistance (Souza Rodrigues et al. 2024), making the species one of the most troublesome weeds across multiple countries (Roberts and Florentine, 2022), and this resistance might represent an early step toward ecological speciation.

Our results are consistent with previous studies that reported a lack of relationship between land-use intensity and phylogenetic divergence (Egorov et al. 2014), while expanding the geographic scope of the analysis to include regions with diverse biogeographical and management contexts. However, it is important to note that our plant assemblages differ from those analysed in Egorov et al. (2014), which focused on managed grasslands shaped by a combination of ungulate herbivore pressure and deforestation (Pärtel et al. 2005), rather than arable weeds sampled within field crops. Therefore, comparisons between the studies should be approached with caution, considering the differences in plant assemblages and ecological context.

Finally, we note that although our dataset is exceptionally comprehensive, it was collected nearly two decades ago, and continued intensification may have further reduced arable weed diversity in certain areas, potentially obscuring some of the patterns reported here. Nonetheless, the patterns examined reflect fundamental ecological dynamics that remain relevant for understanding how plant assemblages respond to agricultural intensification and for informing future management strategies.

Conclusion

In-field AgI plays a significant role in the moderate-to-high levels of taxonomic dissimilarity observed among arable weed assemblages of European farms, with increased intensification driving the exclusion of AgI-sensitive species and the persistence of tolerant ones, resulting in nested assemblages. Therefore, restoring diverse arable weed communities may require promoting species adapted to low-intensity systems and managing competition from persistent AgI-tolerant species. Other factors not considered in this study, such as microenvironmental variability and management legacies, likely underpin the replacement of species between farms, a process that contributes more to the total observed taxonomic dissimilarity than nestedness. Phylogenetic structure metrics showed weak and inconsistent correlations with AgI, likely because the traits associated with AgI may have evolved through distinct and complex evolutionary trajectories long before the surge of AgI in the mid-twentieth century.

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Author contributions RM-V and MBM conceived the ideas, RM-V conducted the analyses, plotted the figures, and led the writing with help from MBM. IG, JJO, TP, TT, JL, TA, ME, FB, VB, WWW, JB and MBM contributed to the sampling design and data collection. All authors read, commented, and approved the final version of the manuscript.

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Data availability The data supporting the findings of this article are available upon request.

Declarations

Competing interests The authors declare no competing interests.

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