RESEARCH ARTICLE

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Agriculture intensification reduces plant taxonomic and functional diversity across European arable systems

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Abstract

1. Agricultural intensification is one of the main drivers of species loss worldwide, but there is still a lack of information about its effect on functional diversity of arable weed communities.

2. Using a large-scale pan European study including 786 fields within 261 farms from eight countries, we analysed differences in the taxonomic and functional diversity of arable weeds assemblages across different levels of agricultural intensification. We estimated weed species frequency in each field, and collected species' traits (vegetative height, SLA and seed mass) from the TRY plant trait database. With this information, we estimated taxonomic (species richness), functional composition (community weighted means) and functional diversity (functional richness, evenness, divergence and redundancy). We used indicators of agricultural management intensity at the individual field scale (e.g. yield, inputs of nitrogen fertilizer and herbicides, frequency of mechanical weed control practices) and at the landscape scale surrounding the field (i.e. number of crop types, mean field size and proportion of arable land cover within a radius of 500 m from the sampling points).

3. The effects of agricultural intensification on species and functional richness at the field scale were stronger than those of intensification at the landscape scale, and we did not observe evidence of interacting effects between the two scales. Overall, assemblages in more intensified areas had fewer species, a higher prevalence of species with ruderal strategies (low stature, high leaf area, light seeds), and lower functional redundancy.

4. Maintaining the diversity of Europe's arable weed communities requires some simple management interventions, for example, reducing the high intensity of field-level agricultural management across Europe, which could be complemented by interventions that increase landscape complexity.

1 | INTRODUCTION

Agriculture is the most widespread land use in Europe, occupying roughly 40% of total land area of the EU-28 (Eurostat, 2018) and harbouring a large part of the continent's biodiversity (Emmerson et al., 2016). Intensification of agricultural management over recent decades has substantially increased crop yields, but the associated environmental costs have been a significant cause for concern for some time (Chamberlain, Fuller, Bunce, Duckworth, & Shrub, 2000; Matson, Parton, Power, & Swift, 1997). Consequently, land use change and agricultural intensification are the principal drivers of species loss worldwide (Green, Cornell, Scharlemann, & Balmford, 2005; Tilman et al., 2001). Agricultural intensification can also affect which species are present in assemblages depending on their traits, therefore changing functional diversity (Cadotte, Carscadden, & Mirotchnick, 2011; Flynn et al., 2009). The loss of diversity can, in turn, affect the structure and functioning of ecosystems, potentially threatening the provision of ecosystem services that sustain our livelihoods (de Bello et al., 2010; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). In this context, arable weeds are particularly important for ecosystem services delivered by pest control agents or pollinators (Brooks et al., 2012; Ebeling, Klein, Weisser, & Tscharntke, 2012; Scherber et al., 2010), providing the resource base in trophic and mutualistic networks in arable systems. As a result, they determine to a high degree the diversity and composition of the associated biota, that is, insects, birds and mammals (Butler et al., 2010; Eraud et al., 2015; Evans, Pocock, Brooks, & Memmott, 2011).

Increases in yields in agricultural production associated with intensification result from changes occurring at two main scales (Emmerson et al., 2016): (a) at the level of the individual field (where practices such as use of high-yielding crop varieties, mechanization, irrigation, and pesticide and fertilizer application directly affect plant communities; Donald, Sanderson, Burfield, & van Bommel, 2006; Geiger et al., 2010) and (b) at the level of the surrounding landscape (processes that lead to smaller species pools and less connectivity, reducing colonization probability; Sirami et al., 2019; Tscharntke et al., 2012). Different taxonomic groups are likely to respond to different scales of intensification because species vary in many ways, including mobility, range size, dispersal ability and sensitivity to agricultural disturbance activities (Billeter et al., 2007). For example, plant diversity can respond more to local management than

to landscape complexity (Aavik & Liira, 2010; Guerrero, Carmona, Morales, Oñate, & Peco, 2014), while the opposite can occur for mobile vertebrates (Gonthier et al., 2014).

Despite their adaptations to the particular selection pressures in agricultural fields (Sutherland, 2004), the diversity of arable weeds has been strongly affected by intensification. The effects of intensification on arable weeds are most noticeable at the individual field scale, where a range of management practices focus on reducing their presence and potential impacts on crop yield (Emmerson et al., 2016; Storkey, Meyer, Still, & Leuschner, 2012). The effectiveness of some of these actions has been called into question, since they are more effective at removing rare plant species than at reducing the densities of competitively dominant and abundant ones (Petit et al., 2016). Here, landscape complexity can play a significant role in maintaining species diversity in arable fields, providing an abundant source of seeds from ruderal habitats and field edges (Gabriel, Thies, & Tscharntke, 2005). Beyond reducing species richness, management intensity does not affect all arable weed species in the same way. Some species with specific traits or trait combinations are better able to cope with high management intensities (Guerrero et al., 2014). Previous studies have shown lower diversity of functional traits in arable weed assemblages from more intensively managed fields, suggesting that intensification is associated with biotic homogenization (Guerrero et al., 2014; Hevia et al., 2016). This biotic homogenization is further compounded by the loss of functional redundancy along the intensity gradient, with more intensified areas hosting assemblages that are more vulnerable to species losses (Carmona, Guerrero, Morales, Oñate, & Peco, 2017).

Differences in climatic conditions and the size and composition of species pools can further complicate the study of intensification effects on diversity. Species identity, community composition, trophic complexity and trait diversity might all differ biogeographically and therefore the effects of agricultural management intensity might differ across biogeographical regions. Despite the urgent need for regional- and landscape-scale (large scale) studies that encompass a larger variety of conditions, most of our understanding about the effects of agricultural management intensity on plant diversity comes from studies performed at field scales (local scales). The few studies analysing the effects of land use change at continental or global scales come from meta-analyses that do not focus exclusively on agricultural management intensity, rather they provide insights from a synthesis of studies with a variety of experimental designs

(Laliberté et al., 2010; Martin et al., 2019). In this sense, coordinated efforts across different countries with common sampling methods are much needed, providing important details of the effects of agricultural intensification on taxonomic and functional diversity (Emmerson et al., 2016).

In this paper, we examine the effects of agricultural intensification, at the local field and landscape level (in a radius of 500 m), on the diversity of arable weeds assemblages in fields of cereal-dominated agroecosystems. We analyse a large-scale dataset originally collected using standardized methods (see Emmerson et al., 2016 for a detailed description of the project), and including nine study areas from eight European countries providing strong gradients in agricultural intensity and environment both within regions and between regions. Within these regions, we selected fields that differ in the values of agricultural management variables that are commonly used as proxies for agricultural intensification. This space-by-time substitution enabled a characterization of differences in the impacts of intensification on local diversity between biogeographical regions. In the present study, we aim to (a) identify the relevant scale (individual field or landscape scale) at which agricultural intensification is most strongly associated with local arable weeds diversity; (b) evaluate whether taxonomic and functional diversity respond in similar ways to intensification; (c) investigate how intensification promotes certain functional trait values, leading to changes in the functional diversity and composition of assemblages and (d) characterize the type of arable weeds communities favoured by current intensification trends.

2 | MATERIALS AND METHODS

2.1 | Study areas, farms and fields

Fieldwork was performed in cereal farms in nine study areas (Sweden, Estonia, Poland, eastern and western Germany, the Netherlands, Ireland, France and Spain). In each study area, 30 farms separated by at least 1 km were selected, and considered to be representative of a gradient of regional agricultural intensification. Given the diversity of agricultural management practices and the scale of management units in the different countries involved in the study, individual farms were considered the ecological unit under study, and for the purposes of the study each was recognized as a set of one or more fields, separated by a distance of not more than 1 km, which were cultivated by the same farmer (owned or leased), and occupying an area not exceeding 1 km^2. These farms were situated in regions between 30 × 30 and 50 × 50 km^2 in area, in order to limit within-region variation in the size of species pools and β-diversity, and to avoid an excessive heterogeneity of landscapes and soil types within each study area. Farms were selected so that the range of cereal productivity in the sample was as large as possible, based on information obtained from the farmers on cereal yields in the 3 years preceding the study, and with a representative and even distribution across the gradient of productivity in each area. Only cereal crops were sampled on each farm (mainly winter wheat: 80% of the fields; if wheat

was not available on the farm, winter barely was used). Sampled fields were never smaller than 1 ha in size nor irrigated. Sampling took place from June to July 2007, and was synchronized using the phenological stages of winter wheat in each study area (i.e. always during the flowering to milk ripening period within each study area). To further avoid phenological effects, the sequence of farm sampling was randomized over the yield gradient within each study area.

For each farm, five sampling points distributed over a maximum of five arable fields were selected for plant sampling. When there were fewer than five fields available, the points were stratified in proportion to size of sampled fields. Sampling points were laid parallel to grassy (never woody) field borders and at 10 m distances from the border towards the field centre. Weeds were sampled in three 2 × 2 m^2 quadrats per sampling point, placed parallel to the field edge and separated 5 m from each other.

2.2 | Vegetation sampling and agricultural management information

We identified the weed species (i.e. all vascular plant species except the crops) present in each sampling quadrat. Then, we pooled the three quadrats within each sampling point, obtaining the frequency of presence of each species in each sampling point. A four-point scale of local abundance was used ranking sampling locations from 0 (absent) to 3 (present in the three quadrats). Following Guerrero et al. (2014), all subsequent analyses were performed at the sampling point level (since we consider the sampling point as representative of the local community of arable weeds, for brevity we will refer to them as 'assemblages' from now on).

We measured six indicators of agricultural management intensity both at the individual field and at the surrounding landscape scales (Table 1). The indicators of agricultural management intensity associated with the individual field scale were assessed by means of questionnaires, undertaken in person with the farmers responsible for managing the sampled fields, and included measures of yield and inputs of nitrogen fertilizer and herbicides. We used digital maps created from remotely sensed images from each study area to estimate the indicators of agricultural management intensity associated with the landscape scale. These landscape scale measures included the size of the focal field and two measures of landscape structure that were quantified within a radius of 500 m around each sampling point, these were mean arable field size and the proportion of arable land cover.

Given the multidimensional nature of agricultural intensification, which encompasses many correlated variables, dimensionality reduction is a common way to estimate it (Carmona et al., 2017; Flohre et al., 2011). Accordingly, following Guerrero et al. (2014), we performed a principal component analysis (PCA) on these indicators of agricultural management intensity. We retained two orthogonal axes that explained 62% of the total variance (Table 1; Figure S1). The first axis (PC1) was related to management practices at the individual field level (contributed by yield, and the number of herbicide and nitrogen fertilizer applications). The second axis (PC2) was related to

TABLE 1 Description of the different agricultural management intensity variables at the field and landscape level used in the study, and their loadings in the selected principal component analysis axes

Variable	Description	PC1 (field)	PC2 (landscape)
Field-level			
Yield	Cereal grain obtained in focal field (tonnes/ha)	0.86	0.02
Amount of herbicide	Total amount of herbicide active ingredients applied on focal field (g/ha)	0.75	0.19
N fertilizer	Total amount of nitrogen applied on focal field (kg/ha)	0.86	−0.08
Landscape level			
Mean field size	Mean size of fields with arable crops within a 500 m radius circle centred on focal field (ha)	−0.01	0.84
Percentage cover of arable crops	Percentage area of arable crops within a 500 m radius circle centred on focal field	−0.03	0.61
Focal field size	Size of each surveyed plot's focal field (ha)	0.16	0.75

the structure of the surrounding landscape (and was defined by sampled field size, mean arable field size and percentage cover of arable crops). We used these axes to produce estimations of agricultural intensity at the local field and landscape level, respectively (Table S1).

2.3 | Functional trait information and diversity estimation

We collected functional traits for the species found in the vegetation surveys from the TRY database (Kattge et al., 2020; Appendix S1). We chose three traits that are related to plant strategy for resource capture and allocation: SLA, vegetative plant height and seed mass (Westoby, 1998). These traits reflect different strategies in plant dispersal, establishment, persistence and response to disturbances (Díaz et al., 2016), and are related to ecosystem functions such as soil multifunctionality, decomposition rate or herbivory (de Bello et al., 2010; Peco, Navarro, Carmona, Medina, & Marques, 2017; Valencia et al., 2018). We estimated the average value for each trait and species after excluding outliers (observations >3 SD away from the species' mean). The averages for each species and trait combination were calculated first within individuals (if multiple measurements were taken from a single individual), then within datasets (if multiple individuals were measured in the same location) and finally within species (if multiple individuals were measured in various locations). In calculations of functional structure, we only considered species for which we had complete trait information, and removed the assemblages when less than 80% of the species in that assemblage had trait information associated with them. This left a total of 335 species and 1,235 assemblages (i.e. sampling points) distributed in 786 fields within 261 farms in the nine study areas.

Preliminary data exploration showed that the raw data for seed mass and plant height were not normally distributed, so these variables were log-transformed to attain normal distributions. In each

assemblage, we used species richness (estimated as the number of species found in each sampling point) as an indicator of taxonomic diversity, and the average trait value (community weighted mean; CWM) for each trait as an indicator of the most frequent trait values, that is, the functional composition of assemblages (Carmona, Mason, Azcárate, & Peco, 2015). Furthermore, we calculated several indicators of functional diversity in each assemblage. We used for this the trait probability density (TPD) approach, which estimates probabilistic functional niches of species and assemblages, which allow afterwards to estimate several aspects of functional diversity (Carmona, Bello, Mason, & Lepš, 2019; Carmona, de Bello, Mason, & Lepš, 2016). Since information on intraspecific trait variability was not available, the centre of each TPDs function was defined by the coordinates corresponding to its three trait values, and the variance around it was estimated by means of a fixed kernel bandwidth of 0.5 SD for each trait (following Lamanna et al., 2014). Subsequently, we estimated the TPD function of each sampling point (TPDc) by calculating a weighted average of the TPDs functions of the species in each assemblage, using their relative frequency as a weighting factor (see Carmona et al., 2016 for further details). The value of a TPDc function for each particular combination of trait values reflects the probability of observing that combination in the considered assemblage.

We then used the R package TPD (Carmona, 2019; Carmona et al., 2019) to estimate several indicators of functional diversity in the assemblages, including functional richness (the amount of functional space occupied by the assemblage; Figure 1a), functional evenness (the evenness in the distribution of the abundance in the functional trait space; Figure 1b), functional divergence (the degree to which the pooled abundance is distributed towards the extremes of the functional volume of the assemblage; Figure 1c) and functional redundancy (the degree to which the species in an assemblage occupy the same functional space; Figure 1d). All these indices are described in detail in Carmona et al. (2019). Both functional richness and functional redundancy are related to species richness (since both indices can only increase as new
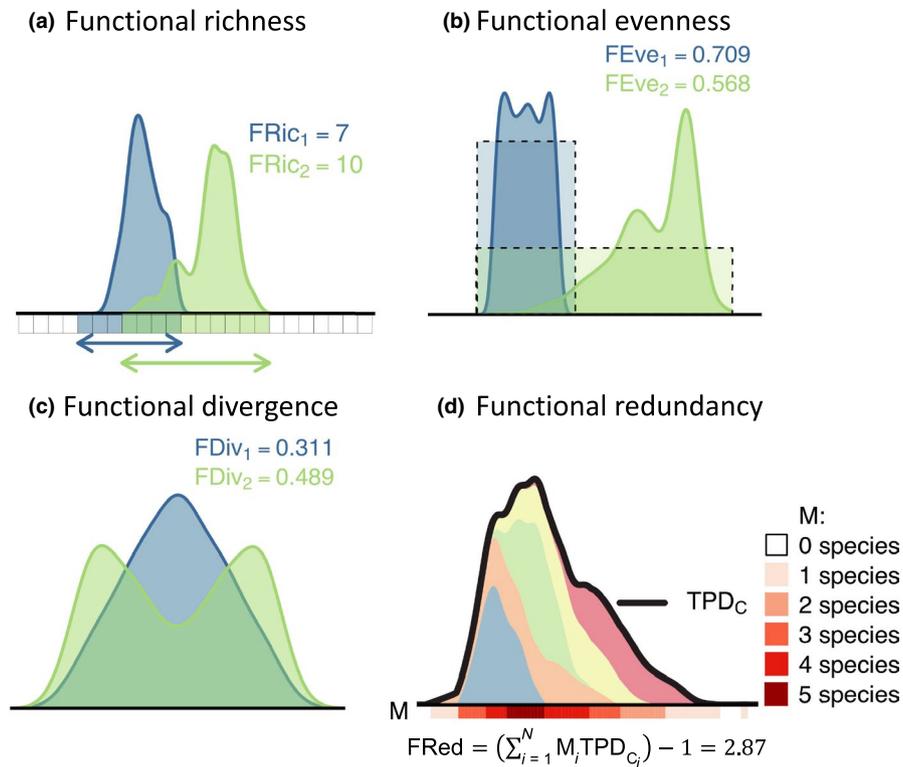
(a) Functional richness

$FRic_1 = 7$
$FRic_2 = 10$

(b) Functional evenness

$FEve_1 = 0.709$
$FEve_2 = 0.568$

(c) Functional divergence

$FDiv_1 = 0.311$
$FDiv_2 = 0.489$

(d) Functional redundancy

M:
☐ 0 species
1 species
2 species
3 species
4 species
5 species

TPD_C

M

$$FRed = \left(\textstyle\sum_{i=1}^{N} M_i TPD_{C_i} \right) - 1 = 2.87$$

FIGURE 1 Illustration of the selected indices of functional structure. In the TPD framework, the functional structure of an assemblage is expressed as a probability distribution (TPDc) whose value in each point in the functional space reflects the relative abundance of the corresponding trait in the assemblage. For simplicity, all examples are shown in a single dimension (1 trait), although in the analyses we have considered a three-dimensional functional space. Functional richness (a) indicates the amount of functional space occupied by assemblages; assemblages with higher functional richness (community 2) display a larger variety of trait values. Functional evenness (b) reflects the uniformity in the occupation of the functional space by an assemblage; assemblages with higher functional evenness (community 1) are more similar to an imaginary assemblage occupying the same functional space in a perfectly even way (which are depicted by discontinuous lines). Functional divergence (c) indicates the degree to which the trait abundances in the assemblages are distributed towards the extremes of the part of the functional space they occupy; assemblages with lower functional divergence (assemblage 1) have a higher concentration of traits close to the centre of gravity of the assemblage in the trait space. Functional redundancy (d) reflects how much different species (indicated by different colours in the figure) occupy the same functional space. This is estimated by dividing the functional space in a large number of cells (N) and then averaging the number of species (M) that are found within each cell, using the abundance of the total distribution (TPDc) as weighting factor. In the example, the functional space of the assemblage is occupied by an average of 3.87 species; after subtracting 1 from that, functional redundancy expresses the average number of species that could be removed from the assemblage without reducing its functional richness. For formal definitions of these indices, see Carmona et al. (2016, 2019)

species are added). To quantify the patterns of association between these indices and to ensure independence from the taxonomic aspect of diversity, we additionally performed two different corrections. In the case of functional richness, we compared the observed value in each assemblage for this index with the values expected under random species assembly processes; for this, we performed a matrix-swap null model, randomizing species within each study area while keeping both row and column sums fixed (permatswap function from the R package VEGAN; Oksanen et al., 2018). We estimated 500 null values of functional richness for each assemblage using this procedure, and then compared them with the observed value using Standardized Effect Sizes (SES; Carmona, Rota, Azcárate, & Peco, 2015; Micó et al., 2020). In the case of functional redundancy, the upper bound of this measure in an assemblage can also be calculated from species richness minus one (S−1); in order to break this correlation, we expressed redundancy in relative terms by dividing it by S−1 (Carmona et al., 2019).

2.4 | Statistical analyses

We examined the relationship between the assemblage level metrics (species richness, functional CWM of the three traits, functional richness, evenness, divergence and redundancy) and agricultural intensity at the field and landscape levels by means of mixed models (with a Poisson distribution in the case of species richness), using the LME4 R package (Bates, Mächler, Bolker, & Walker, 2015). The models included both intensity indicators (scores in the PCA axes) as explanatory variables, and field nested in farm nested in study area as random factors, to account for the hierarchical study design. We explored whether the responses to agricultural intensity were similar across study areas for each response variable by fitting a model with random slopes for both intensity indicators as random slopes within study areas and a model without these random slopes. We compared these two models with different random structures by means of AIC, and kept for

each variable the model with the lowest AIC score (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). For all selected models, we estimated conditional and marginal coefficients of determination using the function r.squaredGLMM from the MuMIn package (Barton, 2016; Nakagawa, Johnson, & Schielzeth, 2017). Conditional R^2 reflects the variance explained by the entire model, including both fixed and random effects, whereas marginal R^2 reflects the variance explained only by the fixed effects, that is, intensity at the field and landscape levels.

3 | RESULTS

All the models including random slopes for intensification had higher AIC values than the models without the random slopes (Table S2). Accordingly, all reported results correspond to the models without random slopes.

3.1 | Species richness

Agricultural intensity had a strong influence on species richness (marginal R^2 = 0.29). In particular, field-level intensity markedly reduced species richness, with a three-fold reduction in the number of species observed in the assemblages from the least-intensified to the most-intensified fields (poisson regression $\beta_{Field} \pm SE$ = −0.38 ± 0.03; p < 0.001; Figure 2). Intensity at the landscape level had a much smaller but still highly significant negative effect ($\beta_{Landscape}$ = −0.08 ± 0.03; p = 0.002; Figure 2) reducing observed species richness. We did not observe a significant interaction between the two levels of intensification (p = 0.19).

3.2 | Functional composition

Agricultural intensity significantly affected the average values of the three selected traits. However, it explained low amounts of variation in all cases (marginal R^2 was between 0.01 and 0.02), with the random effects explaining a much larger proportion (conditional R^2 between 0.67 and 0.73). Similarly, the proportion of variation explained by each level of the random factor differed markedly between traits, with differences between fields and between farms accounting for a majority of variability in plant height (c. 25% each level), whereas most of the variation in SLA and seed mass was between study areas (42% and 39%, respectively). Plant height decreased with field-level intensity (β_{Field} = −0.18 ± 0.06; p = 0.003), whereas average SLA values generally increased (β_{Field} = 0.14 ± 0.05; p = 0.006; Figure 3). However, landscape-level intensity did not have any important effect on these two traits. In contrast, seed mass decreased with intensification at the landscape level, but showed no patterns at the field scale ($\beta_{Landscape}$ = −0.11 ± 0.05; p = 0.016; Figure 3).

3.3 | Functional diversity

As expected, functional richness followed patterns similar to species richness (marginal R^2 = 0.23), decreasing with intensity at the field (β_{Field} = −103.14 ± 8.98; p < 0.001) and at the landscape scale ($\beta_{Landscape}$ = −23.60 ± 8.49; p = 0.006; Figure 3). However, after removing the effect of species richness by means of the null model (functional richness SES), landscape-level intensity ceased to have an effect (Figure S2). In contrast to raw functional richness, functional richness SES increased with intensity at the field level, but overall the effects of intensity on this variable were very small (marginal R^2 = 0.01; Figure S2). Agricultural intensity had a moderate effect on functional evenness (marginal R^2 = 0.08; Figure 3) so that functional evenness increased with intensity at the field scale (β_{Field} = 0.008 ± 0.001; p < 0.001), but not at the landscape scale. Similarly, functional divergence increased with intensity at the field scale (β_{Field} = 0.02 ± 0.003; p < 0.001) and was not significantly related to intensity at the landscape scale. Functional
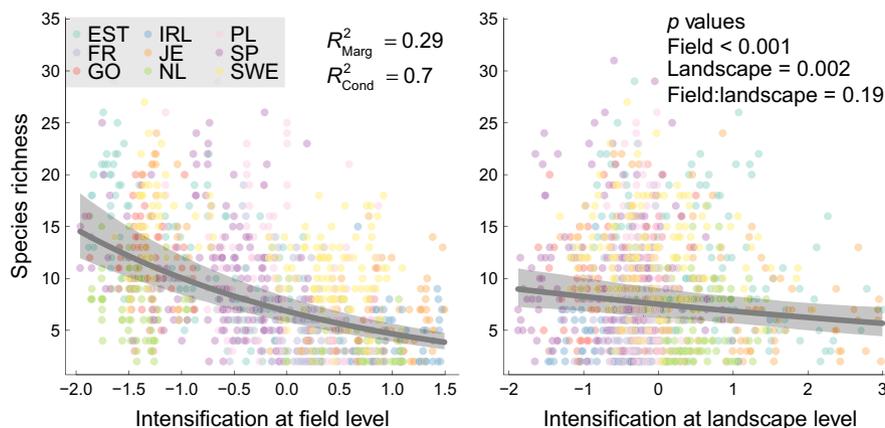

FIGURE 2 Partial regression plots showing the effects of agricultural intensification at the field (left) and landscape (right) levels on weed species richness (mean prediction and 95% confidence intervals), modelled using a generalized mixed model with Poisson distribution. R^2_{Marg} indicates the proportion of variance explained by the fixed effects (field- and landscape-level management intensity and their interaction), and R^2_{Cond} includes both fixed and random effects. Colours indicate the study area to which each point belongs (EST, Estonia; FR, France; Go, Germany (Göttingen); IRL, Ireland; JE, Germany (Jena); NL, the Netherlands; PL, Poland; SP, Spain; SWE, Sweden)
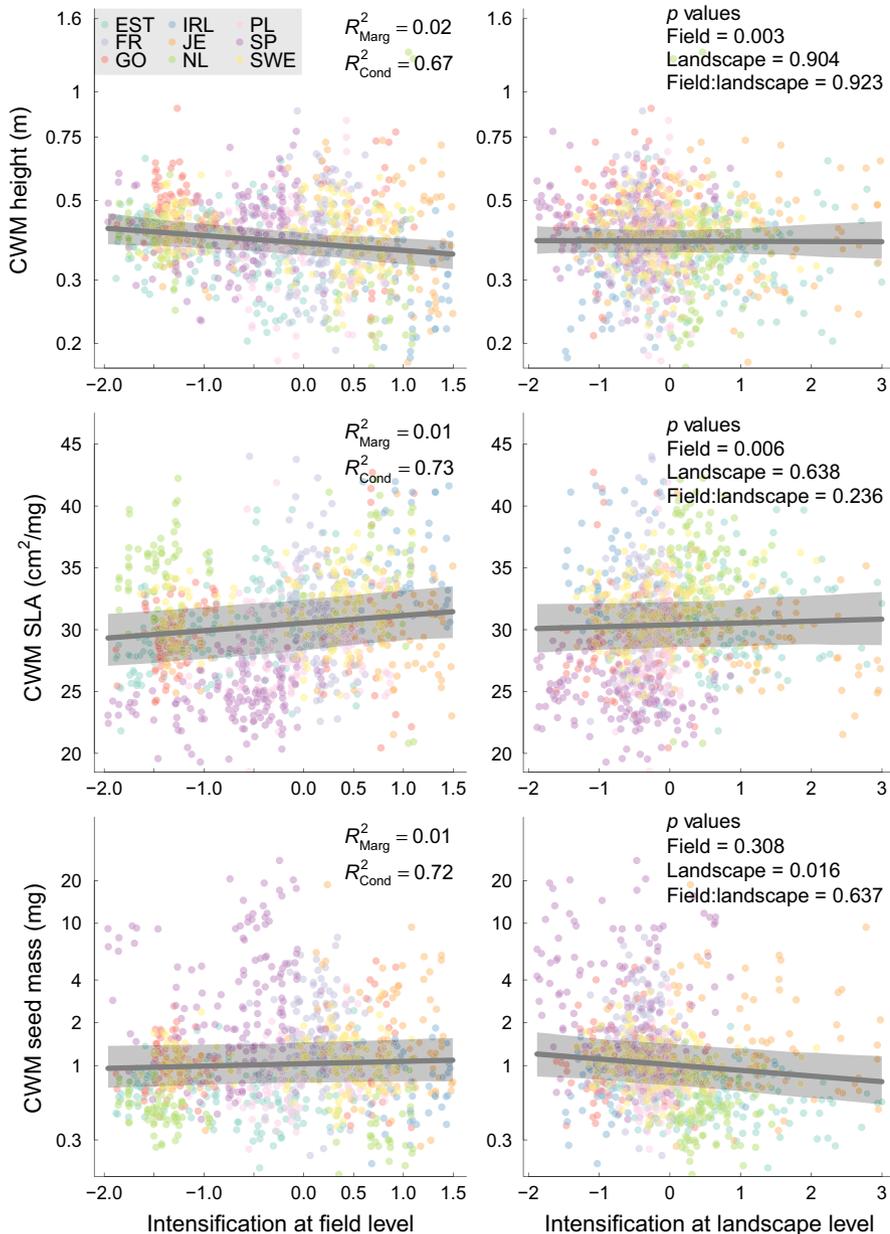
FIGURE 3 Partial regression plots showing the effects of agricultural intensification at the field (left) and landscape (right) levels on functional composition modelled using linear mixed models. Functional composition is represented by the community weighted mean of plant height, SLA and seed mass. R^2_{Marg} indicates the proportion of variance explained by the fixed effects (field- and landscape-level management intensity and their interaction), and R^2_{Cond} includes both fixed and random effects. Colours indicate the study area to which each point belongs (EST, Estonia; FR, France; Go, Germany (Göttingen); IRL, Ireland; JE, Germany (Jena); NL, the Netherlands; PL, Poland; SP, Spain; SWE, Sweden)

redundancy decreased substantially with field-scale intensity (β_{Field} = −0.78 ± 0.06; p < 0.001; Figure 3), but was not affected by intensity at the landscape scale. This negative effect of intensification at the field scale remained significant after correcting for the effect of species richness on redundancy (relative redundancy; Figure S3).

4 | DISCUSSION

Our results show that agricultural intensification had consistently negative effects on the diversity of arable weeds assemblages of European cereal-dominated agroecosystems and that this effect was stronger at local field scales than at the landscape scale. Despite the strong decline of taxonomic diversity associated with agricultural intensification (Figure 2), we found much weaker effects on the functional structure of assemblages (evidenced by the

generally low marginal R^2 values; Figures 3 and 4), due to the high levels of functional redundancy among species that buffered the effects of species loss. Overall, intensification selected for species with ruderal strategies (low stature, high SLA, light seeds; Pierce et al., 2017) so that these traits were more prevalent in assemblages subject to intensification. Ultimately, this selection contributes to lower functional redundancy. These results depended strongly on the level at which intensification was considered: we found evidence supporting the idea that intensification affects weeds diversity mostly through selection operating at the local field scale. Nonetheless, intensification at the landscape scale also had a negative effect on the average seed mass of weeds assemblages, suggesting that species with poor dispersal abilities are selected against in very intensified landscapes.

The relevance of spatial scale remains vitally important for how we manage conservation interventions in agricultural landscapes

FIGURE 4 Partial regression plots showing the effects of agricultural intensification at the field (left) and landscape (right) levels on different indicators of the functional diversity of arable weeds assemblages (functional richness, evenness, divergence and redundancy) modelled using linear mixed models. R^2_{Marg} indicates the proportion of variance explained by the fixed effects (field- and landscape-level management intensity and their interaction), and R^2_{Cond} includes both fixed and random effects. Colours indicate the study area to which each point belongs (EST, Estonia; FR, France; Go, Germany (Göttingen); IRL, Ireland; JE, Germany (Jena); NL, the Netherlands; PL, Poland; SP, Spain; SWE, Sweden)
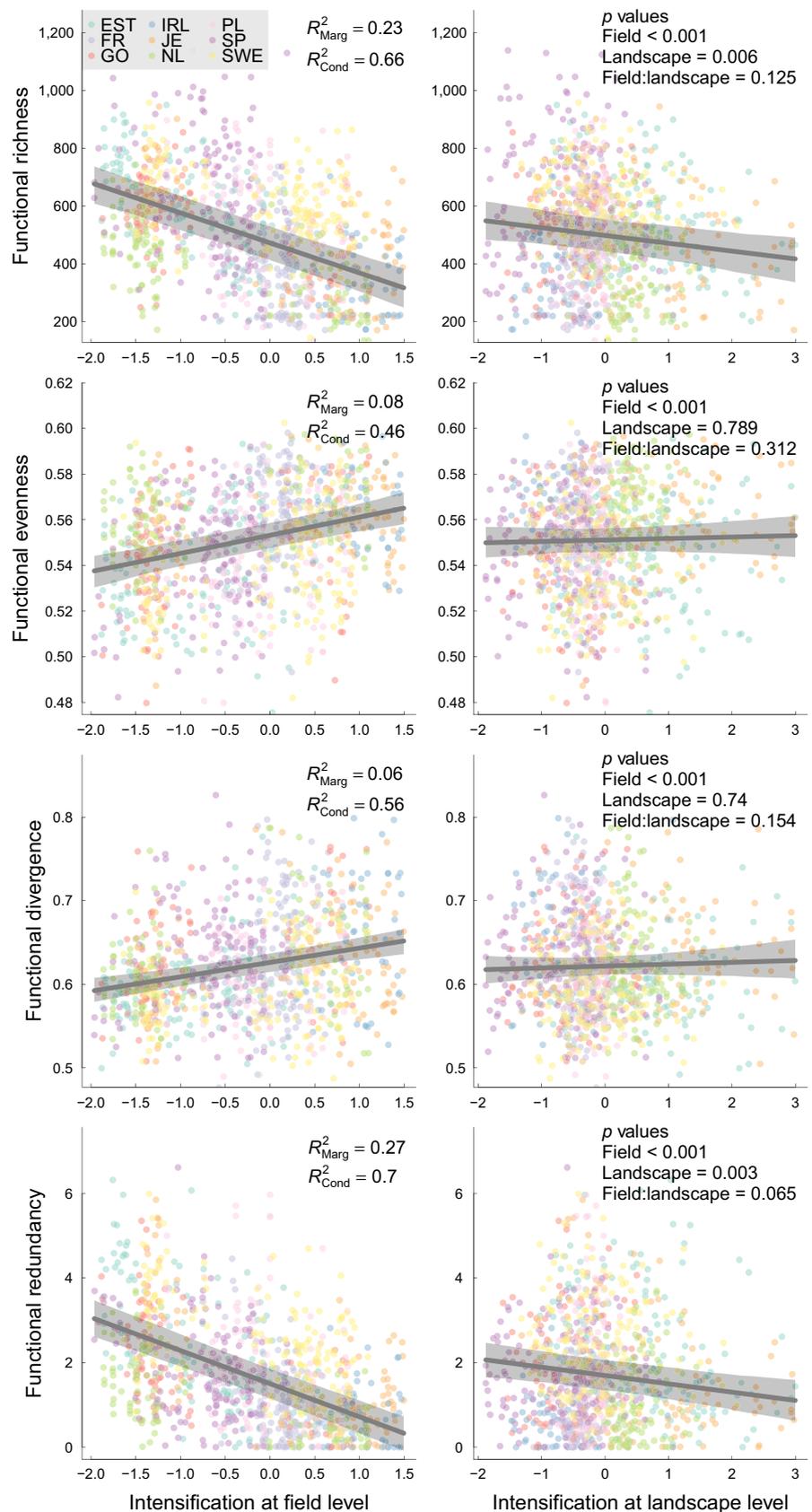
(Emmerson et al., 2016; Petit et al., 2016; Tscharntke et al., 2005). For example, previous work suggests that the most important scale for consideration depends on the mobility of the taxonomic group under study. Whereas birds (Guerrero et al., 2012), carabids (Winqvist et al., 2014) or wild bees (Happe et al., 2018) are primarily influenced by landscape factors, weed diversity seems to be more

strongly determined by field-scale factors (Carmona et al., 2017; Guerrero et al., 2014). However, some recent studies have underscored the importance of the larger-scale factors for arable weeds diversity, either independently or by modulating the effects of local factors (Gabriel et al., 2010; Henckel, Börger, Meiss, Gaba, & Bretagnolle, 2015; Petit et al., 2016; Tuck et al., 2014). Our results do not support this view, since intensification at the landscape scale had little influence on local species richness, and the interaction with the field scale was not significant for any of the studied variables. The contrasting results obtained from different studies could be due to factors such as the position within the field of the considered samples, or the different ways in which landscape-level intensification was measured between studies. For example, the influence of landscape-scale processes is known to decrease as the distance from the edge of the field increases (José-María, Armengot, Blanco-Moreno, Bassa, & Sans, 2010), and the plots considered in this study where relatively far from field edges. Although other studies encompass factors related to field management, but acting at landscape level, such as the proportion of organic fields (Petit et al., 2016), our landscape-level variables measure exclusively landscape structure or complexity based on semi-natural elements (Billeter et al., 2007).

Our results show that the two considered aspects of intensification had different effects on vegetative (SLA and plant height) and regenerative (seed mass) traits. Field-level intensification seemed to select for phenotypes characterized by smaller stature and higher SLA. Plants with low height are better able to cope with physical disturbance associated with tillage (Rota, Manzano, Carmona, Malo, & Peco, 2017; Westoby, 1998), whereas high SLA values are associated with higher relative growth rates (Shipley, 2006). Together, these traits allow plants to complete their life cycles quickly, hence reducing competition with the crop vegetation (Guerrero et al., 2014), and being able to complete their full life cycle before harvest. Furthermore, herbaceous species with high SLA are better adapted to shade conditions and high supplies of nutrients (Westoby, 1998). Although some studies have reported no relationship between intensification and these traits (Fried, Kazakou, & Gaba, 2012; Guerrero et al., 2014), both smaller stature and higher SLA are frequently found in response to agricultural intensification (Kazakou et al., 2016; Solé-Senan, Juárez-Escario, Robleño, Conesa, & Recasens, 2017), in agreement with the expectation that this process selects for ruderal strategies. In this line, it is important to remark that higher N availability is associated with higher SLA values due to the effect of intraspecific variability (He, Chen, Zhao, Cornelissen, & Chu, 2018) so that local measurements should be preferable to assess the effect of intensification on functional diversity. However, the relative importance of considering local trait values, which is critical at local scales (Carmona, Rota, et al., 2015), decreases as spatial scale increases (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011), as is the case of the present study. The fact that species rankings considering traits from databases and local measurements are similar (Kazakou et al., 2014) suggests that our results should be robust to this effect.

5 | CONCLUSIONS

Because of the loss of landscape complexity in intensively managed landscapes, arable weeds assemblages become more isolated and disconnected from seed sources (e.g. grasslands, fallows and field borders) and tend to have lower propagule pressure. Consequently, the negative effect of landscape level intensification on species richness observed in this study is likely to be due to this isolation effect (Damschen et al., 2019). In the present study, average seed mass decreased with intensification at the landscape scale, probably due to the higher dispersal ability of species with small seeds. Small seeds tend to disperse further (Cornelissen et al., 2003), and tend to persist longer in the soil seed bank (Hernández Plaza, Navarrete, & González-Andejar, 2015). Additionally, given equivalent reproductive investment, plants with small seeds produce more seeds (Jakobsson & Eriksson, 2000). For these reasons, plants with smaller seeds might have a dispersion advantage in intensively managed landscapes and might persist longer in the assemblages. Similar patterns have been observed in other habitats (reviewed in Vellend, 2016), but this is, to the best of our knowledge, the first observation in agricultural landscapes.

The reduction in species richness associated with intensification was accompanied by a similar reduction in the functional space occupied by these arable weeds assemblages. The species-rich assemblages at the least intensified end of the gradient had lower functional evenness and divergence than the assemblages from more intensified fields. This means that the distribution of trait values in the more diverse assemblages tended to be more clumped (see Figure 1). This interpretation was further confirmed by the observed reduction in functional redundancy with intensification. Overall, we found clear evidence showing that agricultural intensification acts by selecting against (or at least reducing the abundance of) functionally redundant species. This, in turn, implies that the functional structure of these systems can resist, relatively well, the loss of species associated with agricultural intensification (Carmona et al., 2017). However, the observed reductions in redundancy were higher than expected for similar levels of species loss (Figure S3), which suggests that functionally unique species are more sensitive to intensification than species with more commonly occurring trait values. The extirpation of more unique species could have profound impacts if they are also important for ecosystem functioning, as found in other systems (Mouillot et al., 2013). Overall, lower functional redundancy due to intensification is likely to increase the vulnerability of these systems to other impacts, such as climate change (Rader, Bartomeus, Tylianakis, & Laliberté, 2014) or biological invasions (Galland et al., 2019; Loiola et al., 2018).

European arable weeds communities are threatened by agricultural intensification (Weisser et al., 2017). Their decline weakens fundamental ecosystem functions (Knops et al., 1999), thus compromising the provision of key ecosystem services, and even the profitability of certain productive activities associated with agriculture (Emmerson et al., 2016; Gaba, Gabriel, Chadœuf, Bonneu, & Bretagnolle, 2016). Our results highlight the need to extensify the field-level agricultural management throughout Europe, that is,

TABLE 2 Summary of the expected effects of agricultural intensification across Europe on taxonomic diversity, functional composition (community weighted means) and functional diversity considered in this study

	Field level	Landscape level
Taxonomic diversity		
Species richness	Communities with fewer species	Communities with fewer species
Functional composition		
Plant height	Shorter plants with reduced dispersal ability	—
SLA	Faster growing plants (more vulnerable to predators and parasites)	—
Seed mass	—	Light-seeded plants with high dispersal but lower seedling survival
Functional diversity		
Richness	Communities with reduced variation in functional trait values	Communities with reduced variation in functional trait values
Evenness	Communities where all trait values are more evenly represented	—
Divergence	Communities where the most abundant species have different trait values	—
Redundancy	Communities with fewer plants of similar trait values	—

reduction of input amounts and frequency of ploughing and other mechanical operations, and longer rotation cycles that incorporate fallow periods. Arable weeds communities would also benefit from the promotion of higher landscape complexity, which could be achieved through maintaining or developing extensive use of some cereal fields (e.g. by promoting organic agriculture or by using fallows), and would support species with poor dispersal abilities. Although dynamic interpretations should be made carefully when using space-for-time substitution studies (Damgaard, 2019), the use of data collected following a standardized protocol across a continental scale, and the selection of fields with relatively homogeneous characteristics (crop type, climate, soils) within study areas, make the results of this study particularly valuable. Our study provides expectations about the changes in farmland plant community structure and functional composition in the face of increasing agriculture intensification across Europe (see Table 2). This knowledge could be used to guide and inform management interventions at the appropriate spatial scales aimed at preventing further species loss and mitigating potential impacts on ecosystem services linked to global change processes.

AUTHORS' CONTRIBUTIONS

C.P.C., I.G., B.P., M.B.M. and J.J.O. conceived and initiated the study; M.B.M., J.J.O., I.G., T.P., T.T., J.L., T.A., M.E., F.B., P.C., V.B., W.W.W. and J.B. coordinated data collection from their study regions and/or directly collected data; C.P.C. analysed the data; C.P.C., I.G., B.P., M.B.M. and J.J.O. wrote the paper, with inputs from all authors.

DATA AVAILABILITY STATEMENT

Data have been deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.2rbnzs7k5 (Carmona et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.