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RESEARCH PAPER

Increasing habitat connectivity in agricultural landscapes as a weed management strategy reconciling ecology and agronomy

Léa Uroy[a,b,c,d,*], Cendrine Mony[a,c], Aude Ernoult[a,c], Audrey Alignier[b,c]

[a]*UMR CNRS 6553 ECOBIO, University of Rennes, Avenue du Général Leclerc, 35042 Rennes Cedex, France*
[b]*UMR 0980 BAGAP, INRAE-ESA-Institut Agro Rennes Angers, 65 Rue de Saint-Brieuc, 35042 Rennes Cedex, France*
[c]*LTSER "Zone Atelier Armorique", 35042 Rennes Cedex, France*
[d]*Université de Toulouse, École d'Ingénieurs de Purpan, INPT, UMR Dynafor 1201, 75 voie du TOEC, f-31076 Toulouse Cedex, France*

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Abstract

While studies have explored how habitat amount drives weed assemblages in agroecosystems, knowledge remains limited of the effects of habitat connectivity. The response-effect trait framework provides insights into the mechanisms underpinning the relationship between landscape structure and the taxonomic diversity and abundance of weed assemblages. This study evaluated how habitat connectivity and habitat amount affect weed diversity and abundance in winter cereal fields, and whether these effects are driven by the functional composition of weed assemblages. We sampled weeds in 27 winter cereal fields. We measured habitat connectivity and habitat amount provided by wooded, grassland and cropland elements. We selected five traits related to the dispersal, establishment, and competitive abilities of weed species likely to respond to landscape structure: seed number per plant, type of reproduction, seed dry mass, plant vegetative height and seed germination rate. The functional composition of weed assemblages was assessed using community weighted mean trait values. Weed diversity and abundance were used as proxies of weed management. The taxonomic approach did not reveal any effect of landscape structure on weed diversity and abundance. Only the grassland elements that contributed to habitat connectivity, and to a lesser extent to habitat amount, drove the functional composition of weed assemblages. High habitat amount favoured species with many seeds, while high habitat connectivity favoured species with fewer seeds, a higher ability to reproduce vegetatively and higher seed germination rates. In turn, higher seed germination rates increased weed evenness and reduced weed abundance. Some of these relationships were influenced by the presence of rare species. Overall, high connectivity provided by grassland elements increases weed evenness and reduces weed abundance by shaping weed functional composition. Our study suggests that land-use planning policies that enhance the connectivity provided by grassland elements could be considered as a weed management strategy reconciling ecology and agronomy.

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Keywords: Habitat isolation; Habitat amount; Landscape structure; Functional traits; Weed assemblages; Weed diversity; Weed management; Trait-based approach

*Corresponding author.
E-mail address: lea.uroy@purpan.fr (L. Uroy).

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Introduction

Over the last half-century, agricultural intensification and subsequent landscape homogenization led to a drastic loss of biodiversity and the deterioration of key ecosystem services provided by arable lands (Robinson & Sutherland, 2002; Tilman et al., 2001). While arable weeds support important ecosystem functions (*e.g.*, the maintenance of pollination, limiting soil erosion, and providing food and shelter for higher trophic levels) in agricultural landscapes (Bretagnolle & Gaba, 2015; Marshall et al., 2003; Pimentel et al., 1995), they have long been considered a major problem for farmers due to competition with crop affecting yields.

Weed assemblages have been for a long time assumed to be driven only by agricultural practices. More recently, studies demonstrated the effect of landscape structure on weed diversity and abundance (Petit et al., 2013). These two parameters were selected as proxies of weed management (Dainese, Montecchiari, Sitzia, Sigura, & Marini, 2017), considered here as the inner agroecosystem resistance to weed colonization. Rare weeds can be an indicator of an ecosystem's health, and their diversity depends also

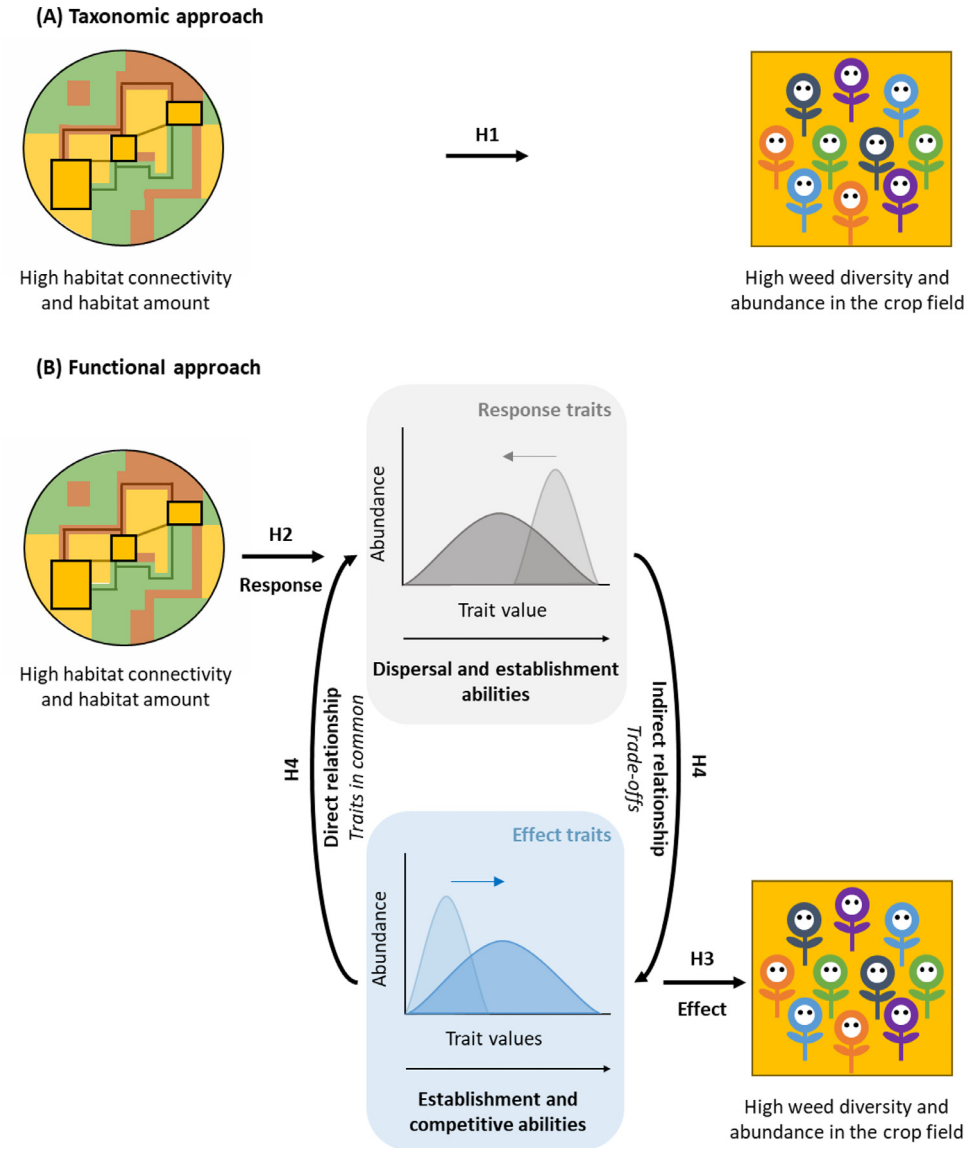


Fig. 1. Illustration of our four hypotheses (H1, H2, H3 and H4) on how habitat connectivity and habitat amount might influence weed diversity and abundance in the crop fields based on (A) taxonomic (H1) and (B) functional approaches (H2, H3 and H4). H1: High habitat connectivity and high habitat amount increase weed diversity and abundance in crops. H2: High habitat connectivity and high habitat amount favor species with trait values conferring low dispersal abilities and/or with low ability for seedling establishment (*i.e.*, response traits to habitat connectivity and habitat amount). H3: Aggregated trait values of traits conferring high establishment and competitive abilities of the seedlings increase weed diversity and abundance (*i.e.*, effect traits regarding the weed diversity and abundance in crops). H4: Some of the response traits to habitat connectivity and habitat amount are also effect traits regarding the weed diversity and abundance in crops. This latter relationship can be direct due to traits in common involved in dispersal, establishment and competitive abilities of the seedlings or indirect due to traits involved in trade-offs.

on landscape structure (Solé-Senan et al., 2014). While the habitat amount of landscape elements, a descriptor of landscape composition, defined as the proportion of habitat (*e.g.,* the proportion of wooded, grassland and cropland elements) is widely used as a surrogate of landscape structure in weed studies (see references therein Petit et al., 2013), our understanding of how habitat connectivity affects weeds remains limited. Yet, landscape ecologists have demonstrated that connectivity is of key importance in structuring plant assemblages (Damschen et al., 2019; Haddad et al., 2015). High connectivity increases seed dispersal, decreasing the probability of local extinction in fragmented agricultural landscapes (Taylor, Fahrig, Henein, & Merriam, 1993; Wilson & Willis, 1975). By contrast, low connectivity decreases seed dispersal, reducing (re-)colonization of habitat patches, thereby generally disadvantaging species with trait values conferring low colonization abilities such as low seed number (Uroy, Ernoult, & Mony, 2019; Zambrano et al., 2019).

The response-effect trait framework proposes to relate plant assemblage responses to the environmental changes and their effect on ecosystem functions based on species traits (Lavorel, McIntyre, Landsberg, & Forbes, 1997). The effect of environmental changes (at both the field and landscape scale) on plant responses is predicted by *response traits*, while the effect of these changes on ecosystem functions is predicted by *effect traits*. This framework has been applied to weeds so far at the field scale (Bàrberi et al., 2018; Gaba et al., 2017) but should also provide insights into the ecological mechanisms between landscape structure and the diversity and abundance of weeds in crops. However, few studies have attempted to define either weed response traits (Alignier, Bretagnolle, & Petit, 2012; Fried, Villers, & Porcher, 2018) or both response and effect traits to landscape structure (Robleño, Storkey, Solé-Senan, & Recasens, 2018; Solé-Senan, Juárez-Escario, Robleño, Conesa, & Recasens, 2017). This study investigated how habitat connectivity and habitat amount provided by several landscape elements (*i.e.*, wooded, grassland and cropland elements) affect weed management (*i.e.*, total species richness, evenness and mean total cover) in winter cereal fields. Specifically, we tested the following hypotheses.

First, we hypothesize that high habitat connectivity and high habitat amount provided by different landscape elements increase the likelihood of many weed species to disperse and to establish in new crop fields (*i.e.,* mass effect, Shmida & Wilson, 1985) and hence, might increase weed diversity and abundance in crops (Fig. 1A, hypothesis 1).

Second, weed species are likely to exhibit different responses to habitat connectivity and habitat amount depending on their ability to disperse in space and to establish. Species with traits conferring low dispersal abilities and/or with low ability for seedling establishment are expected to be promoted by high habitat connectivity and high habitat amount. If so, traits related to dispersal and/or with seedling establishment abilities would be response traits to habitat connectivity and habitat amount (*e.g.*, Zambrano et al., 2019, Fig. 1B, hypothesis 2). Low dispersal abilities can correspond to species with low number of potential dispersers (*e.g.,* low seed number) and/or a short dispersal distance. Short dispersal distance may result from high seed mass, low plant height and high investment in vegetative reproduction despite some exceptions exist for this latter assumptions (*i.e.,* alien species, Barney, 2006; Duquette et al., 2016; Pyšek & Prach, 1993). Low ability of seedling establishment can correspond to species with low germination rates and low seed mass.

Third, the ability of weeds to colonize the available space in the crop field efficiently is dependent on the establishment and competitive abilities of the seedlings. A high ability for seedlings to establish and develop despite frequent disturbances (*e.g.,* tillage, herbicide application) may be promoted by high germination rates, important vegetative reproduction (Bond & Midgley, 2001; Gross, Suding, & Lavorel, 2007; Klimešová & Klimeš, 2003) and high plant height (Violle et al., 2009). Aggregated values of these traits (*i.e.*, germination rates, type of reproduction, plant height) reflecting high establishment and competitive abilities might increase weed diversity and abundance in crops, and could therefore be considered effect traits (Fig. 1B, hypothesis 3).

Fourth, we investigated the consequences of shifts in the functional composition of weed assemblages induced by habitat connectivity and habitat amount on weed diversity and abundance in crops. Several potential response traits to habitat connectivity and habitat amount can also be traits that, in turn, affect the establishment and competitive ability of seedlings, and thus weed diversity and abundance in crops. This relationship can be either direct due to traits in common involved in dispersal, establishment and competitive abilities of the seedlings, or indirect due to the inevitable trade-offs between species traits (*e.g.*, competition-colonization trade-off, Levins & Culver, 1971). As a result, some of the response traits to habitat connectivity and habitat amount are supposed to be effect traits regarding the weed diversity and abundance in crops (Fig. 1B, hypothesis 4).

Materials and methods

Study area and field selection

This study was conducted in the LTSER "Zone Atelier Armorique" (ZAAr) site (130 km^2), which is located in Brittany, northwestern France (48° 36′ N, 1° 32′ W). This study site is a hedgerow network (*bocage*) landscape characterized by mixed dairy farming and cereal production.

We selected 27 winter cereal fields (wheat or barley) distributed across the study site, with at least 250 m between

any two cereal field edges (Fig. 2A). The selected fields were of similar area (mean: 1.81 ha, range: 0.55–4.38 ha) and representative of conventional winter cereal fields of the study area. They were of similar crop succession (i.*e.*, cultivated as cereals after ploughing of a grassland in 2013, 2014 or 2015) and conducted with similar farming practices (*i.e.,* one ploughing operation, one to two fertilizer inputs and one to three herbicide applications). This standardization was based on interviews with farmers and land-cover maps of the ZAAr database.

Assessment of habitat connectivity and habitat amount

Land-cover maps of the ZAAr raster database were constructed at a high resolution (5 × 5 m) from aerial imagery based on nine categories: grassland, grassy strip, maize, cereal, other crops (*e.g.*, rapeseed), woodland, built area, road and water. We obtained the complete wooded network (*i.e.,* woodlands and hedgerows) from the Kermap raster database (5 × 5 m resolution).

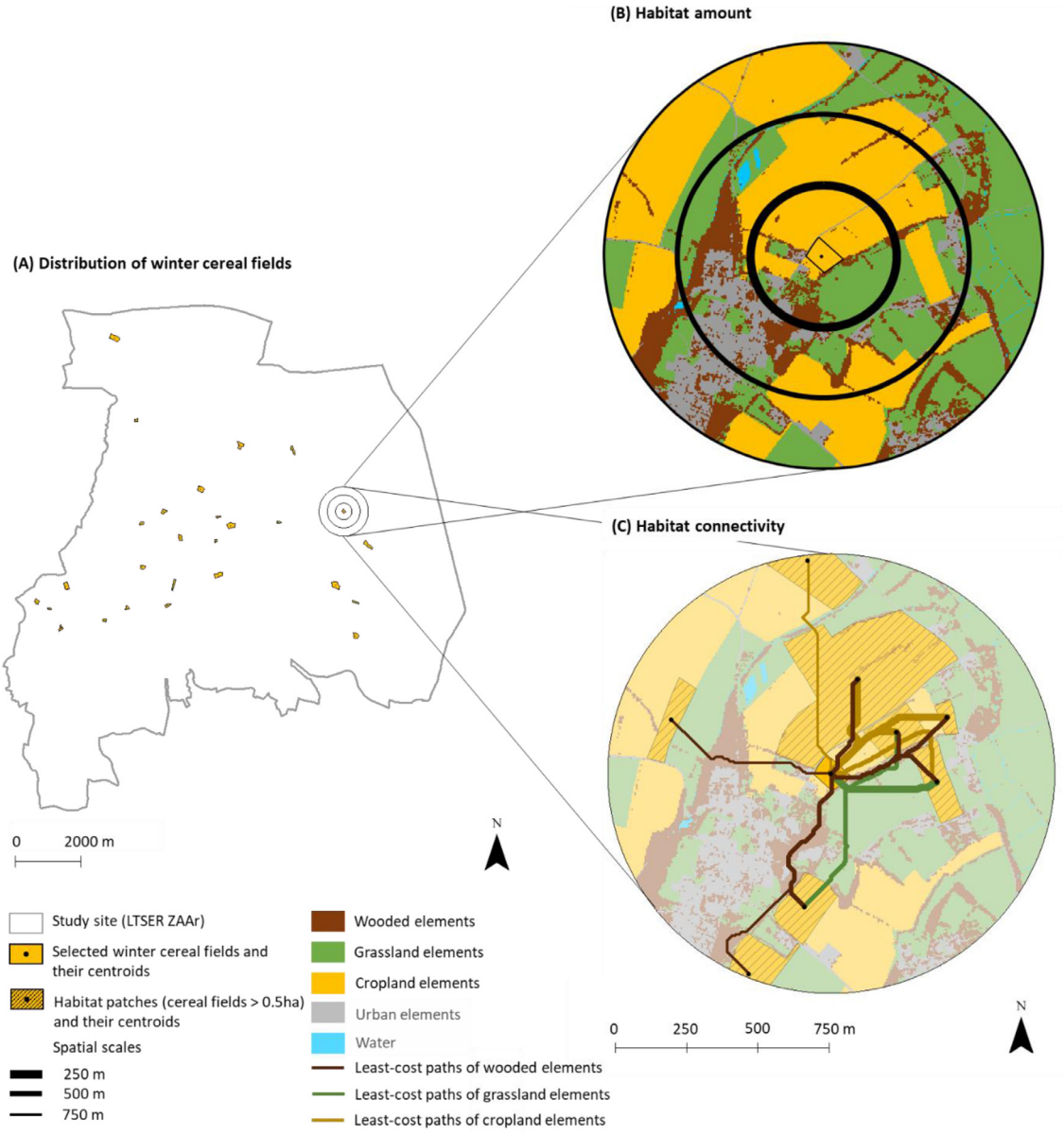


Fig. 2. Illustration of (A) the 27 winter cereal fields distributed throughout our study site, the LTSER "Zone Atelier Armorique", northwestern France, and the three spatial scales (250 m, 500 m, and 750 m) used to assess (B) habitat amount and (C) habitat connectivity provided by wooded, grassland and cropland elements (see map symbols). The shaded map symbols (urban elements and water) correspond to the elements that were not considered because of their low percentage of total cover in the study area.

We assessed habitat connectivity and habitat amount as provided by three dominant landscape elements in agricultural landscapes: wooded elements (woodlands and hedgerows, 22% of the study area; 2016 Kermap database), grassland elements (grasslands and grassy strips, 33% of the study area; 2017 ZAAr database) and cropland elements (maize, cereal, and other crops, 43% of the study area; 2017 ZAAr database). Urban elements (built areas and roads) and water cover correspond to a network of small villages and small streams. They were not considered because of their low percentage of total cover in the study area (8 and 1% of the study area; 2017 ZAAr database). Habitat connectivity and habitat amount were measured around the centroid of each winter cereal field at three spatial radii scales: 250 m (*i.e.*, local scale), 500 m (*i.e.*, intermediate scale) and 750 m (*i.e.*, large scale) (Fig. 2B, C). These three spatial scales were related to the range of spatial scales at which weed species are affected by landscape changes (Gaba, Chauvel, Dessaint, Bretagnolle, & Petit, 2010).

Habitat connectivity

Habitat connectivity was calculated using graph theory-based habitat reachability metrics (Saura & Pascual-Hortal, 2007). The graph theory modeling method was based on least-cost path analysis (Adriaensen et al., 2003) that identify the potential dispersal path of plant individuals between two habitat patches. This path depends on the resistance to dispersal between habitat patches.

We considered all cereal fields in 2017 with an area > 0.5 ha as habitat patches, with adjoining cereal fields belonging to the same patch (n = 564 habitat patches, including the selected winter cereal fields). We considered the inter-patch dispersal distances as a function of the proportion of wooded, grassland and cropland elements. We thus created resistance maps for each landscape element type (three resistance maps, in total). Resistance values were calculated as the reverse of the proportion of the considered landscape element type in a moving circular window (see Appendix A1 for more details). Then, we calculated the inter-patch distance between each pair of habitat patches from each resistance map as the cumulative cost of the least-cost path using the Graphab 2.2.6 software (Foltête, Clauzel, & Vuidel, 2012). The "proportion of total potential dispersal flux in the landscape" connectivity index (Saura & Rubio, 2010) of each selected winter cereal field was calculated for each type of inter-patch distance (*i.e.*, woodland, grassland and cropland elements) and for each spatial scale considered using Conefor 2.6 (Saura & Torné, 2009) (see Appendix A2 for calculations).

Habitat amount

Habitat amount was evaluated using the proportion of each type of landscape element surrounding each selected winter cereal field within 250 m, 500 m and 750 m radius circular buffers using FRAGSTATS v4 (McGarigal, Cushman, & Ene, 2012).

The distribution of habitat connectivity and habitat amount provided by each landscape element for each spatial scale are summarized in Appendix A: Table 1. We checked for correlations between landscape variables (Appendix A: Table 2) and considered that there was no major collinearity (rho < |0.7|; Dormann et al., 2013), except between (i) the habitat amount and the habitat connectivity provided by grassland elements at 250 m and 500 m and (ii) the habitat amount provided by grassland elements and the habitat amount provided by cropland elements at all scales.

Weed data

Weed sampling

We performed weed surveys in the 27 winter cereal fields during June and July 2018. The percent cover of each herbaceous species was recorded using ten plots of 2 x 2 m, the total area of which corresponding to the minimal recommended sampling area for weed assemblages (Hanzlik & Gerowitt, 2016; Mueller-Dombois & Ellenberg, 1974). Plots were evenly distributed within the field, with at least 10 m from each other to account for the spatial heterogeneity of weeds in fields (Cardina, Johnson, & Sparrow, 1997). The outermost plots were at least 10 m from the field border to avoid edge effects. Weed surveys were performed by one observer to minimize bias among the 27 winter cereal fields. Nomenclature followed the French taxonomic register TAXREF v12.0 (available at: https://inpn.mnhn.fr/program/referentiel-taxonomique-taxref).

Functional composition of weed assemblages

We selected five functional traits linked to (i) dispersal, (ii) establishment and (iii) competition (Table 1 and Appendix A: Table 3). Traits were gathered from the TRY (Kattge et al., 2011) and Biolflor (Kühn, Durka, & Klotz, 2004) databases: seed number per plant (SNPP), type of reproduction (ToR), seed dry mass (SDM), plant vegetative height (PVH) and seed germination rate (SGR). These traits were chosen as potential response traits to habitat amount and habitat connectivity amount (*i.e.,* linked to dispersal and seedling establishment) that can, in turn, affect the weed diversity and abundance in winter cereal fields through their effect on the establishment and competitive ability of seedlings (*i.e.,* effect traits). To do so, we restrict our analysis to a set of traits (i) used to be involved in dispersal, establishment and competitive abilities of the seedlings or (ii) involved in trade-offs. Concerning continuous traits, several trait values for a given trait and for a given species could be available in databases. Thus, trait values with an error risk ≤ 4 (*cf.* Kattge et al., 2011) were averaged per trait and per species (see Appendix A3 for details). Trait distributions are summarized in Table 1. The correlations between the five

Table 1. Overview of the five functional traits selected for this study. SE = standard error of the mean. *semi-quantitative trait, [1] log-transformed trait, [2] logit-transformed trait.

Processes	Functional traits	Availability (%)	Description and (units)	Distribution of functional traits before any transformation	
				Mean ± SE	Min - Max
Dispersal	Seed number per plant[1]	89	(1/plant)	4665.40 ± 981.11	10.00 – 56,536.00
Dispersal, establishment and competition	Type of reproduction*	100	Allocation to vegetative reproduction 1: by seed; 2: mostly by seed, rarely vegetative; 3: by seed and vegetative; 4: mostly vegetative, rarely by seed	1.81 ± 0.11	1.00 – 4.00
Dispersal and establishment	Seed dry mass[1]	98	(mg)	2.01 ± 0.51	0.02 – 28.54
Dispersal and competition	Plant vegetative height[1]	100	Maximum vegetative height (m)	0.40 ± 0.03	0.08 – 1.68
Establishment	Seed germination rate[2]	88	Germination efficiency (%)	93.32 ± 0.87	70.00 – 100

selected traits were either non-significant or low (-0.35 ≤ *rho* ≤ 0.29, Appendix A: Table 4). Continuous traits were then either log- or logit-transformed to correct for skewness. The functional composition of weed assemblages was assessed at the field scale (*i.e.*, accounting for all species recorded in the ten plots) using the community weighted mean (CWM) trait value. The CWM is defined as the mean trait value weighted by the relative abundance of each species (*i.e.,* aggregated values of a given trait). We calculated the CWM trait value for each trait and for each winter cereal field using the "FD" R package. To obtain additional information on the functional characteristics of weeds, the life form and the life span for each species were also collected from the Biolflor database (Kühn et al., 2004).

Table 2. Taxonomic (total species richness, Piélou's total evenness, and mean total cover) and functional (community weighted means [CWMs] for each trait considered) characteristics of weed assemblages. These metrics were calculated at the field scale, accounting for all species recorded in the ten plots (N = 27). SE = standard error of the mean. [1] logit-transformed metric. [2] log-transformed trait based metric, [3] logit-transformed trait based metric.

	Distribution of metrics before transformation	
	Mean ± SE	Min – Max
Taxonomic diversity and abundance		
Total species richness	15.33 ± 1.56	3.00 – 33.00
Piélou's total evenness	0.59 ± 0.04	0.10 – 0.92
Mean total cover[1]	19.94 ± 3.68	0.80 – 78.75
Functional composition (CWMs)		
Seed number per plant[2]	8.23 ± 0.23	6.22 – 10.31
Type of reproduction	1.59 ± 0.08	1.02 – 2.64
Seed dry mass[2]	-1.80 ± 0.21	-3.72 – 0.24
Plant vegetative height [2]	-1.34 ± 0.05	-1.67 – -0.81
Seed germination rate[3]	2.03 ± 0.12	1.15 – 3.48

Weed management

For each winter cereal field, we used the diversity and the abundance of weed assemblages at the field scale (*i.e.*, accounting for all species recorded in the ten plots) as proxies of weed management (Dainese et al., 2017). We assessed diversity using total species richness and Piélou's total evenness using the "vegan" R package. We assessed abundance as the mean total cover. The selected metrics were not or not overly correlated (*rho* ≤ |0.66|, Appendix A: Table 5). The mean total cover was logit-transformed to correct for skewness. None of the selected metrics were spatially auto-correlated (Moran's I test, $p > 0.05$). The similarity in weed composition between each pair of winter cereal fields was also measured with the Sørensen index ($S_{sør}$) using the "ade4" R package to obtain additional information on the taxonomic characteristics of weed assemblages. Because the "ade4" R package computes dissimilarity (d) as $\sqrt{1 - S_{sør}}$, we applied the following transformation: $S_{sør} = (- d^2 + 1)$ to convert dissimilarity (d) into a similarity index. The higher the Sørensen index ($S_{sør}$), the higher the similarity between a given pair of winter cereal field.

Statistical analyses

Before the statistical analyses, all variables were centered and scaled to allow for comparisons of regression coefficients among and within models.

First, we used multiple ordinary least square (OLS) regression models to assess the effect of habitat connectivity and habitat amount provided by different landscape

elements (*i.e.*, woodland, grassland and cropland elements) as independent variables on weed diversity (total species richness and Piélou's total evenness) and abundance (mean total cover) in winter cereal fields for the three spatial scales considered (250 m, 500 m and 750 m) (hypothesis 1). Second, we used multiple OLS regression models to assess the effect of habitat connectivity and habitat amount provided by different landscape elements as independent variables on the functional composition of weed assemblages for each trait (CWMs of SNPP, ToR, SDM, PVH and SGR as dependent variables) for the three spatial scales (hypothesis 2). Third, we used multiple OLS regression models to assess the effect of the functional composition of weed assemblages for each trait considered as independent variables on weed diversity (total species richness and Piélou's total evenness) and abundance (mean total cover) in winter cereal fields (hypothesis 3). This procedure allows to identify the aggregated trait values that were significantly influenced by habitat connectivity and/or habitat amount and, in turn, that significantly influenced weed diversity and abundance. In other words, the traits that were both response and effect traits were identified (hypothesis 4). Finally, we performed a path analysis (Wright, 1934) to calculate how habitat connectivity and/or habitat amount affected the weed diversity and abundance in winter cereal fields *via* the functional composition. We calculated a compound path by multiplying (i) the standardized regression coefficient of the model relating habitat connectivity and habitat amount to functional composition with (ii) the standardized regression coefficient of the model relating functional composition to weed diversity and abundance in winter cereal fields. Compound paths indicate the functional composition-mediated influence (sign and magnitude) of habitat connectivity and/or habitat amount on weed diversity and abundance in winter cereal fields.

All of these models were performed using model-averaging methodology to account for uncertainty in the model selection process (Burnham & Anderson, 2002). Full models were tested for multicollinearity. Despite correlations between some of the variables, none of the independent variables showed a variance inflation factor indicative of overly multicollinearity (*i.e.,* exceeding 10, Hair, Black, Babin, Anderson, & Tatham, 2014). Due to our small sample size (N = 27), we built all possible linear models based on all additive combinations of up to three candidate independent variables. Models were ranked by the Akaike's information criterion corrected for small sample sizes (AICc). We generated the full model-averaged estimates of the independent variables using the 95% confidence set weighted by Akaike weights (Burnham & Anderson, 2002). Homoscedasticity and normality of residuals for each model were graphically explored. We considered independent variables significant if the 95% confidence intervals did not overlap with zero. Finally, we calculated the percentage of explained variance for the most parsimonious model (*i.e.*, with the smallest AICc) of the confidence set.

We also checked whether and how the effect of connectivity and habitat amount on weed assemblages was affected by rare species. Although removing rare species can diminish our ability to detect the impact of landscape structure on weed assemblages (Cao, Williams, & Williams, 1998), we performed all statistical analyses by removing species that were present in fewer than 5% of the winter cereal fields (*i.e.*, one field), an approximate rule of thumb in multivariate analysis (McCune & Grace, 2002), corresponding to 22 species in total that were removed from the dataset.

All statistical analyses were performed in R. 3.5.1. Model averaging was performed using the "MuMIn" R package.

Results

Characteristics of weed assemblages

In total, 80 herbaceous species were recorded. The most common species were *Juncus bufonius* L., *Poa trivialis* L. (both present in 81.5% of fields), *Poa annua* L. (70.4%), *Senecio vulgaris* L., and *Stellaria media* (L.) Vill. (51.9%) (Appendix A: Table 6). Almost half of the species (48.8%) recorded was strictly annual (Appendix A: Table 6). The similarity (Sørensen index) in weed composition between each pair of winter cereal fields was 0.32 ± 0.01 (mean ± SE), and ranged from 0 to 0.68. The taxonomic and functional characteristics of weed assemblages are provided in Table 2. Those of weed assemblages after removing rare species from the dataset are provided in Appendix A: Table 7.

Effect of habitat connectivity and habitat amount on weed management

Overall, habitat connectivity and habitat amount did not influence total species richness, Piélou's total evenness, and mean total cover. This phenomenon was observed regardless of the spatial scale considered (Fig. 3 and Appendix A: Table 8) and even after excluding rare species from the dataset (Appendix A: Table 9).

Effect of habitat connectivity and habitat amount on the functional composition of weed assemblages

Only habitat connectivity and habitat amount provided by grassland elements significantly affected the functional composition of weed assemblages. Specifically, only the community weighted means (CWMs) of three traits were related to the connectivity provided by grassland elements: seed number per plant (SNPP), type of reproduction (ToR) and

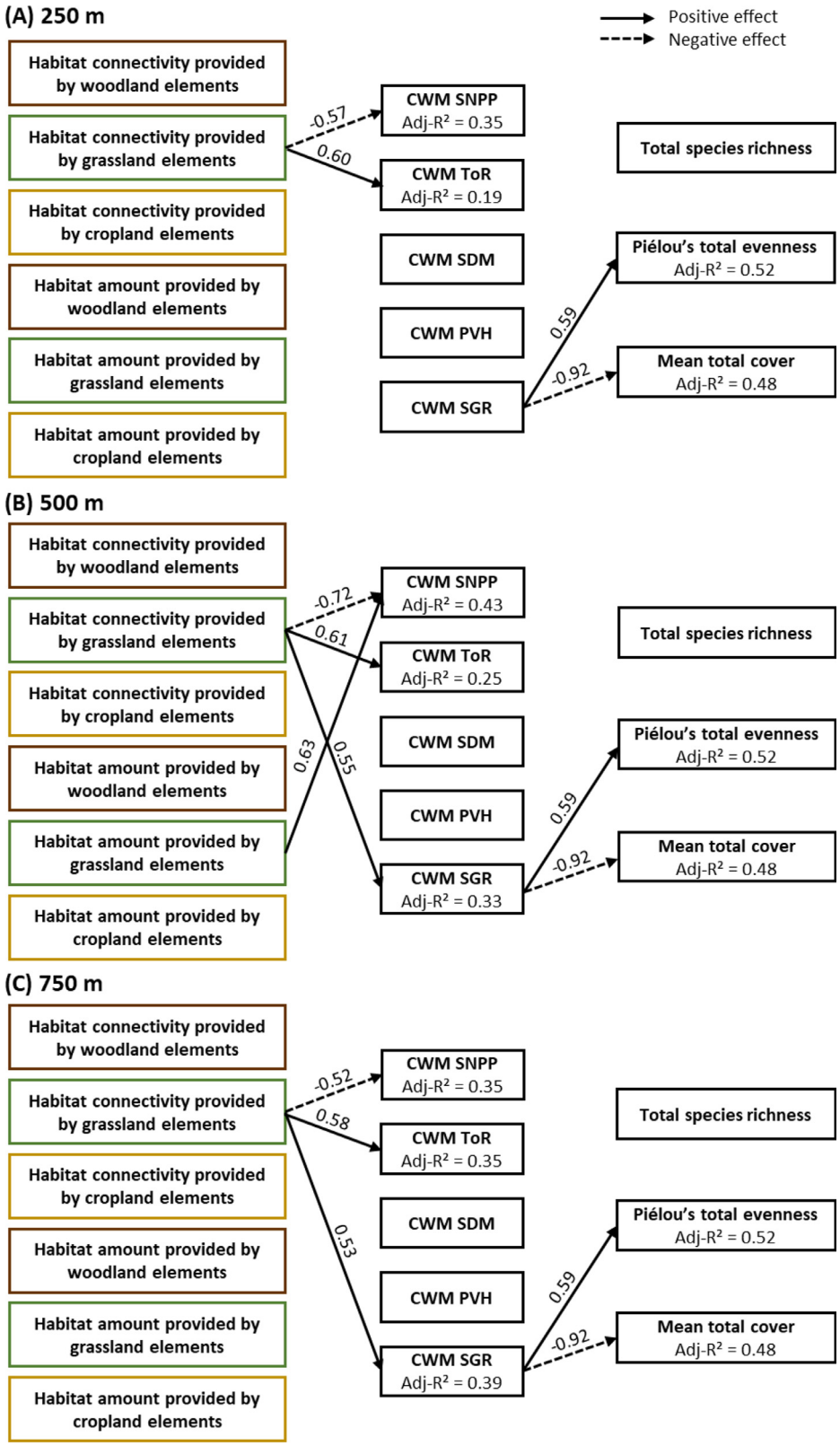


Fig. 3. Overview of the significant effects of (i) habitat connectivity and habitat amount (left column) at (A) 250 m, (B) 500 m, and (C) 750 m on the community weighted mean (CWM) trait values for five traits (middle column) (ii) CWM trait values on total species richness, Piélou's total evenness, and mean total cover of weeds (right column). The traits considered are: seed number per plant (SNPP), type of reproduction (ToR), seed dry mass (SDM), plant vegetative height (PVH), and seed germination rate (SGR). Both dependent and independent variables were calculated at the field scale (N = 27). Effects are indicated as the standardized regression coefficients of the significant model; namely, the sign and magnitude of the effect. Solid lines indicate positive effects while dotted lines indicate negative effects. Explained variance (Adj-R^2) is indicated in the box of each dependent variable for significant models. See details in Appendix A: Table 8, 10 and 12.

seed germination rate (SGR) (Fig. 3 and Appendix A: Table 10). The community weighted means of seed number per plant decreased as connectivity increased. The community weighted means of reproduction type increased with connectivity, meaning that high habitat connectivity was associated with a higher ability to reproduce vegetatively. The community weighted means of seed germination rate increased when connectivity increased, but only at 500 m and 750 m. Only the community weighted means of seed number per plant were positively related to the habitat amount provided by grassland elements at the 500 m scale. We also noted negative effects of the habitat amount provided by grassland and cropland elements at 750 m on the community weighted means of seed germination rates after removal of rare species, in addition to the positive effect of the habitat connectivity provided by grassland elements previously observed at this scale (Appendix A: Table 11).

Effect of the functional composition of weed assemblages on weed management

None of the community weighted mean trait values influenced total species richness of weed assemblages (Fig. 3 and Appendix A: Table 12). The community weighted means of seed germination rate strongly affected the Piélou's total evenness and the mean total cover of weed assemblages. Higher community weighted means of seed germination rate led to higher Piélou's total evenness and lower mean total cover. The community weighted means of seed germination rate affected only the mean total cover of weed assemblages when removing rare species (Appendix A: Table 13).

Effect of habitat connectivity and habitat amount on weed management via functional composition

As the community weighted means of seed germination rate (i) were driven by the habitat connectivity provided by grassland elements at 500 m and 750 m and (ii) affected Piélou's total evenness and the mean total cover of weed assemblages, we obtained two trait-mediated effects of habitat connectivity on (i) Piélou's total evenness and (ii) the mean total cover of weeds in crop fields. Specifically, habitat connectivity provided by grassland elements at 500 m and 750 m increased Piélou's total evenness [0.32 at 500 m, *i.e.,* (0.55 × 0.59) and 0.31 at 750 m, *i.e.,* (0.53 × 0.59)] and declined the mean total cover [-0.51 at 500 m, *i.e.,* (0.55 × -0.92) and -0.49 at 750 m, *i.e.,* (0.53 × -0.92)] (Fig. 3B, C, Appendix A: Tables 10 and 12). After removing rare species, only one trait-mediated effect of habitat connectivity, but two trait-mediated effects of habitat amount on the mean total cover of weeds in crop fields were detected (Appendix A: Tables 11 and 13). Habitat connectivity provided by grassland elements at 500 m and 750 m still declined the mean total cover of weeds [-0.61 at 500 m, *i.e.,* (0.62 × -0.99) and -0.58 at 750 m, *i.e.,* (0.59 × -0.99)] but did not affect Pielou's total evenness in crop fields. Habitat amount provided by grassland elements and by cropland elements at 750 m increased the mean total cover of weeds [0.95 for grassland elements, *i.e.,* (-0.96 × -0.99) and 0.70 for cropland elements, *i.e.,* (-0.71 × -0.99)] (Appendix A: Tables 11 and 13).

Discussion

Grassland elements drive the functional composition of weed assemblages

Contrary to what we expected, habitat connectivity and habitat amount provided by wooded and cropland elements (except when removing rare species) did not influence the functional composition of weed assemblages, but grassland did. The surprising absence of effect of cropland elements was probably due to a threshold effect. The high amount of cropland elements in the landscape surrounding crop fields (between 44.5 and 48.5% on average, depending on the spatial scale considered; Appendix A: Table 1) might indeed not be sufficiently limiting to impact the functional composition of weed assemblages in which rare species are found. By studying the respective effects of wooded and grassland elements rather than their combined effects (*e.g.,* Liira et al., 2008), we demonstrated that only grassland elements influence the functional composition of weed assemblages. The lack of effect of wooded elements could be due to the fact we also included woodlands and hedgerows into wooded elements. Contrary to hedgerows (Boutin, Baril, & Martin, 2008; Dainese et al., 2017), woodlands are less likely to provide refuges or suitable corridors for the dispersal of weeds given their high affinity for nutrient-rich, sunny, and dry habitats (Bourgeois et al., 2019). This positive effect of hedgerows might have been masked as they represented here a small proportion of wooded elements. Apart from these hypotheses, the effects of wooded and cropland elements may be relatively unimportant for weeds when local factors exert very strong control over species recruitment, as in conventional winter cereal fields. The conventional farming system of winter cereal fields, by selecting among arriving species those tolerant to disturbances, may thus explain this present − but weak − landscape effect, especially for rare species, trumped by farming practices.

Among traits related to dispersal and establishment, only one trait influenced how weeds responded to habitat amount, giving only little support to the fact that such traits constitute response traits to landscape structure (second hypothesis). A high habitat amount of grassland around crop fields favoured weed species with high seed production. This result can be explained by the fact that *Juncus bufonius* L. dominated

weed assemblages. This species has an abundant and persistent seedbank and establishes primarily in trampled microsites of grasslands (Matějková, Diggelen, & Prach, 2003). Thus, the huge seed production of *Juncus bufonius* L. (more than 30 000 seeds *per* plant, Kattge et al., 2011) that can lie dormant in soils for up to 100 years (Peter, 1894 *in* Thompson, Bakker, & Bekker, 1997) might facilitate its ability to reach winter cereal fields through mass effect. Of note, when removing rare species, another trait, seed germination rate, was involved in weed response to habitat amount, with a high amount of grassland and cropland elements favoured species that had low seed germination rates.

Conversely, several traits linked to dispersal and seedling establishment were involved in the response of weed species to habitat connectivity. Thus, habitat connectivity might override habitat amount in shaping the functional composition of weed assemblages, minimally supporting the Habitat Amount Hypothesis (Fahrig, 2013), especially for assemblages in which rare species are present. Specifically, high habitat connectivity provided by grasslands favoured species that produced few seeds, but also species that had a higher ability to reproduce vegetatively and that had high seed germination rates. The sensitivity of species producing a low number of seeds to connectivity loss (*i.e.,* being disfavoured by connectivity loss) is well recognized for forest and grassland plants (*e.g.,* Evju, Blumentrath, Skarpaas, Stabbetorp, & Sverdrup-Thygeson, 2015; Verheyen, Vellend, Calster, Peterken, & Hermy, 2004). Our study gives support to the fact that this phenomenon may extend to weed species. However, the response of clonal plants to connectivity loss does not appear to be straightforward: our findings, in line with the study of Kolb & Diekmann (2005), contradict previous studies showing that clonal plants are resistant to connectivity loss (*i.e.,* being unaffected or favoured by connectivity loss; Lindborg, 2007; Piessens, Honnay, Nackaerts, & Hermy, 2004). Vegetative reproduction is considered an alternative life cycle that allows the persistence of local species without sexual reproduction Eriksson (1996), particularly if a population has been isolated (Eriksson & Ehrlén, 2001). Vegetative reproduction alone without any other traits ensuring long-term persistence (*e.g.,* persistent seed bank) leads to a certain risk of local extinction (Honnay & Bossuyt, 2005). Yet, 100% of three species that reproduce mostly vegetatively and 92% of 24 species that reproduce either vegetatively or sexually had a transient or short-term persistent seed bank in our study (LEDA database, Kleyer et al., 2008).

Our findings also contrast with previous studies demonstrating that plants resistant to connectivity loss display high seed germination rates (Favre-Bac et al., 2017). Habitat connectivity did not affect seed mass nor plant height in our study. However, detecting the effect of habitat connectivity on seed mass and plant height is difficult (Evju et al., 2015; Piessens, Honnay, & Hermy, 2005; Schleicher, Biedermann, & Kleyer, 2011). Their relative roles in dispersal distance are indeed still subject to debate (Thomson, Moles, Auld, & Kingsford, 2011) and they are also involved in further stages of plant development before efficient colonization (establishment, competition). Overall, we showed that traits promoting seedling establishment and/or local persistence, rather than traits conferring high dispersal abilities, are those which contributed most to the sensitivity of plants to connectivity loss.

Interestingly, our findings suggest that studying the local landscape surrounding winter cereal fields is less relevant than studying the landscape at an intermediate or a large scale to understand how landscape structure affects the functional composition of weed assemblages. The greater the extent of landscape, the stronger the ability to detect the processes involved in weed responses to landscape structure. These results provide new insights into the scale of effects (*i.e.,* the spatial extent at which landscape structure best predicts assemblage responses; Jackson & Fahrig, 2012) of weed species, contradicting one previous study which showed that the local landscape best predicts taxonomic responses (200 m, Gaba et al., 2010) but supporting previous studies which highlighted that the landscape at a large scale predicts taxonomic (1000 m, José-María, Armengot, Blanco-Moreno, Bassa, & Sans, 2010) and functional (1000 m, Solé-Senan et al., 2014, 2017) responses.

Germination of weeds reduces their abundance and increases their diversity in winter cereal fields

Weed diversity (here, evenness) and abundance in winter cereal fields were driven by a trait related to seedling establishment, namely seed germination rate, giving support to the fact that traits related to establishment, and competitive abilities constitute effect traits regarding the weed diversity and abundance (third hypothesis). We found that low seed germination rates decreased weed evenness (except after the removal of rare species) and increased weed abundance in winter cereal fields. These low germination rates might cause high seed dormancy of weeds (Colbach, Dürr, Roger-Estrada, Chauvel, & Caneill, 2006), which is used to synchronize germination (Baskin & Baskin, 2014) when crops are sown. Weed species that maximize seedling establishment within winter crops – thereby preventing other species from establishing themselves – germinate and emerge at around the time that the crop is sown (*i.e.,* between October and November in our study area) (Gunton, Petit, & Gaba, 2011). Thus, seed germination rate can be considered a response trait that drives weed management and thus, the functioning of agroecosystems. Despite the ability to maximize seedling establishment and to resist to competitive pressure (by resprouting and spreading laterally), allocation to vegetative reproduction did not predict weed evenness and abundance. This result was unexpected because, in many habitats, greater vegetative reproduction (*i.e.,* both vegetative growth in cultivation and greater lateral expansion) was correlated with higher abundance at both the local and

regional scales (Herben, Nováková, & Klimešová, 2014). Using a combination of clonal traits, for example by integrating the presence of an underground vegetative bud bank (Klimešová & Klimeš, 2003, 2007) or clonal expansion (Ross & Harper, 1972), might be more appropriate to describe and elucidate the effect of vegetative reproduction on weed evenness and abundance. Plant height did not influence weed management, possibly due to the overriding effect of the winter cereal canopy which limits the height to which weeds grow (Borgy et al., 2016) and hence increases the abundance of small weeds (Perronne, Gaba, Cadet, & Le Corre, 2014).

Finally, none of the other traits involved in dispersal and seedling establishment (*i.e.* seed number, seed mass) influenced weed evenness and abundance. Although seed rain does influence the taxonomic characteristics of assemblages in many habitats (Mouquet, Leadley, Mériguet, & Loreau, 2004; Myers & Harms, 2009), the disturbances and the competition imposed by farming practices in conventional winter cereal fields might override dispersal processes.

Using the response-effect trait framework improves our understanding of weed management

We did not reveal any effect of habitat connectivity and habitat amount on weed diversity and abundance in winter cereal fields. When using the functional approach (response-effect trait framework), we demonstrated that enhancing habitat connectivity provided by grassland elements at an intermediate or large scale (500 m and 750 m) could increase the germination success of weeds and, thus, increase their evenness – except when rare species are not considered – and reduce their abundance. This result supports our fourth hypothesis for this particular trait, which was that some of the response traits to habitat connectivity and habitat amount can be effect traits regarding the weed diversity and abundance in winter cereal fields. Higher species evenness associated with lower biomass production (in grasslands, Mulder et al., 2004) or total species abundance (in crops, Cordeau et al., 2017) has previously been reported in experimental systems, and appears in our study to be the result of the presence of rare species. This result may support the hypothesis that more diverse weed assemblages are less competitive, and less prone to dominance by a few highly competitive, herbicide-resistant weeds (Storkey & Neve, 2018). We also showed that habitat amount did not affect weed evenness and abundance when rare species were considered. Therefore, land-use planning policies that enhance the connectivity provided by grasslands could be considered a weed management strategy that reconciles both ecological and agronomical issues, *i.e.,* maximizing weed diversity whilst reducing weed abundance. Of note, such policies could be favourably perceived by farmers as they might profit from a reduction of weed abundance without compromising the allocation of fields to crop or livestock production (*i.e.,* pasture or hay). We are aware that these recommendations may be considered in the light of the limitations related to the methodology applied for this observational study. Indeed, we focused only on traits likely to respond to landscape structure, thereby restricting the analysis to a set of traits related to the dispersal and establishment abilities that are involved in trade-offs. We also might have underestimated the effect of landscape structure on aboveground weed assemblages as they result from an intense local environmental filtering due to conventional management (*e.g.*, tillage, nitrogen fertilization, herbicide application). This calls for future research to expand further this framework in less-disturbed systems, such as field edges or organic fields. The reduced intensity or the lack of nitrogen fertilization and herbicide applications may allow revealing stronger or other landscape effects on weed diversity and abundance, by exerting a lower establishment limitation among species that arrive (Gabriel, Roschewitz, Tscharntke, & Thies, 2006 but see Roschewitz, Gabriel, Tscharntke, & Thies, 2005).

Overall, this study presents a new approach to predict the effect of landscape-scale processes on ecosystem functioning in agricultural landscapes, by expanding the response-effect trait framework to these large-scale assembly processes. Distinguishing traits that are only response traits to landscape-scale processes from the traits that are both response and effect traits regarding weed management, we provide one of the first evidences that high connectivity maximises weed diversity whilst reduces weed abundance by favouring species with higher seed germination rates. Further expansion of this framework should advance our understanding of whether and how functional changes in weed communities in response to landscape modifications are likely to influence agroecosystem functioning.

Data availability

Data and R scripts used for this study are available on Figshare (https://figshare.com/s/b2a17efa7f8affb5540e. doi: 10.6084/m9.figshare.14743464). Land-cover and hedgerow network maps are available on Osuris (https://accueil.osuris.fr/).

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.03.003.

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