RESEARCH ARTICLE

Weed communities are more diverse, but not more abundant, in dense and complex bocage landscapes

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Abstract

1. Bocage landscapes are characterized by a network of hedgerows that delimits arable fields. Such landscapes provide many ecosystem services, including biodiversity conservation, but their effects on weed communities remain largely unknown. Bocage landscapes could affect weed communities through two main processes: plant spillover from hedgerows and increased environmental heterogeneity in arable fields. These bocage effects are also likely to vary between farming systems (conventional vs. organic) due to differences in management practices.

2. We sampled weed communities more than 20 m from field margins in 74 arable fields (37 per farming system). Fields were located along two independent landscape gradients of total length of hedgerows (with or without a shrub layer) and organic farming cover, in Brittany (France). We analysed the effect of 'bocage' (i.e. the density and complexity of hedgerow networks) and farming systems at field and landscape scales on species and functional diversity of weed communities. Further, we used fidelity to non-crop habitats and Ellenberg indicator values to assess the 'plant spillover' and 'environmental heterogeneity' hypotheses, respectively.

3. Weed communities were more diverse and more abundant in organic farming systems. In addition, weed communities were more diverse, but not more abundant, in denser and more complex bocage landscapes. 'Bocage' increased species diversity of weeds, but also community-weighted variance of specific leaf area, plant height and seed mass. Positive effects of 'bocage' on weed diversity were driven by increased environmental heterogeneity rather than spillover of transient species from hedgerows. 'Bocage' effects were independent of farming systems at field and landscape scales.

4. *Synthesis and applications.* Maintaining diverse weed communities is key to agroecological weed management and biodiversity conservation in agricultural landscapes. Farmers are often concerned that hedgerows harbour competitive plants spreading into field edges, thereby increasing weed pressure. However, our study shows that dense and complex bocage landscapes promote weed diversity in field cores, most likely by increasing environmental heterogeneity.

Thus, bocage landscapes could actually enhance ecosystem services provided by weed communities and reduce weed-crop competition.

1 | INTRODUCTION

Through landscape simplification, decreased crop diversity and increased agrochemical use, agricultural intensification led to a dramatic loss of weed diversity (Fried et al., 2009; Meyer et al., 2013), and evolution of herbicide resistance in weeds (Neve et al., 2009). Since 2010, around 3 million tons of herbicides are used each year worldwide to eliminate weed species (FAO, 2021), in most cases regardless of their actual impact on crop yield and ecosystem service provision. However, only a small proportion of weed species causes significant yield loss (Adeux et al., 2019; Marshall et al., 2003). For example, of 306 main weed species described in Germany (Hofmeister & Garve, 1998), only 26 were defined as problematic. On the contrary, weeds can be a major asset for biodiversity conservation and ecosystem service provision in agroecosystems (Marshall et al., 2003). There is growing evidence that maintaining weed diversity enhances multifunctionality and sustainability of agroecosystems (Gaba et al., 2020; Liebman et al., 2021). In addition, weed diversity is key for agroecological weed management. First, diversified weed communities provide a wider range of habitat and trophic resources for natural enemies, which promotes biological control of weeds themselves (Gaba et al., 2020; Schumacher et al., 2020). Second, diversification of weed communities can prevent the dominance of competitive weeds and limit yield loss due to weed-crop competition (Adeux et al., 2019; Dornelas et al., 2009; Storkey & Neve, 2018), most likely by promoting greater niche differentiation and resource partitioning between weeds and crops (Smith et al., 2010).

In a seminal review, MacLaren et al. (2020) emphasized that agricultural intensification selects for fast-growing and tall weeds with ruderal to competitive strategies. These authors suggested that reduced resource availability and increased diversity in management practices and habitats should promote weed communities with more diverse life strategies. Hedgerows may play a role in this regard, but their effects on weed communities remain understudied, especially at landscape scale. Hedgerows can provide many ecosystem services, including sustainable food and biomass production, soil and water protection, carbon sequestration, and biodiversity conservation (Montgomery et al., 2020). On the other hand, farmers are often concerned that hedgerows harbour competitive plants spreading into arable fields (Alignier et al., 2020). Hedgerows are relatively stable habitats that can support high plant diversity (Vanneste et al., 2020). Thus, plant spillover from hedgerows could increase weed cover and diversity in arable fields. Under conventional farming, plant spillover is typically restricted to field edges, due to limited dispersal distances and regular disturbances including tillage operations and agrochemical use (Figure 1a) (e.g. Marshall, 1989; Metcalfe et al., 2019). Plant spillover could extend over larger areas under organic farming given the absence of herbicide and chemical fertilizer treatments (Fried et al., 2022), but studies are lacking. Further, plant spillover is associated with an increased proportion of 'transient' species in arable fields (Metcalfe et al., 2019). These species are not typical 'resident' weeds that emerge from a permanent seedbank, but species that rely on regular dispersal from adjacent source habitats. As such, transient species are adapted to lower disturbances and lower resource availability and characterized by a more competitive or stress-tolerant strategy. On the other hand, hedgerows could influence weed communities through another overlooked process. Hedgerows affect field microclimate (e.g. wind speed, light, temperature, frost), soil parameters (e.g. organic matter, nitrogen flows), and water cycle (e.g. soil and atmospheric moisture, water flows) (Figure 1b) (e.g. Forman & Baudry, 1984; Sánchez et al., 2010). Further, the intensity of hedgerow effects varies with the distance from hedgerows, their features (e.g., dimensions, permeability), their orientation and their spatial configuration in the landscape. This can result in a high degree of environmental heterogeneity in arable fields, providing a broader range of ecological conditions for weed species. Niche differentiation and resource partitioning would then allow more species to coexist and reduce the dominance of competitive weed species (Dornelas et al., 2009).

Most studies assessing the effects of semi-natural habitats on weed communities are restricted to conventional farming (e.g. Alignier et al., 2017; Dainese et al., 2017; Metcalfe et al., 2019). However, 'bocage' effects on weed communities may vary between farming systems (conventional vs. organic, at field and landscape scales). On the one hand, one could expect more pronounced effects of 'bocage' in an organic farming context, given the absence of agrochemical disturbances that prevent germination and growth of many plant species (Gabriel et al., 2010; Metcalfe et al., 2019). On the other hand, 'bocage' effects could be limited in an organic farming context, where arable fields already harbour high levels of diversity (Roschewitz et al., 2005).

Our objective was to assess the effects of 'bocage' (i.e. the density and complexity of hedgerow networks) on weed communities in field cores, and to investigate potential interactions with farming systems at field and landscape scales. In addition to the taxonomic approach, we used a functional approach to assess whether bocage landscapes can mitigate the selection for ruderal to competitive
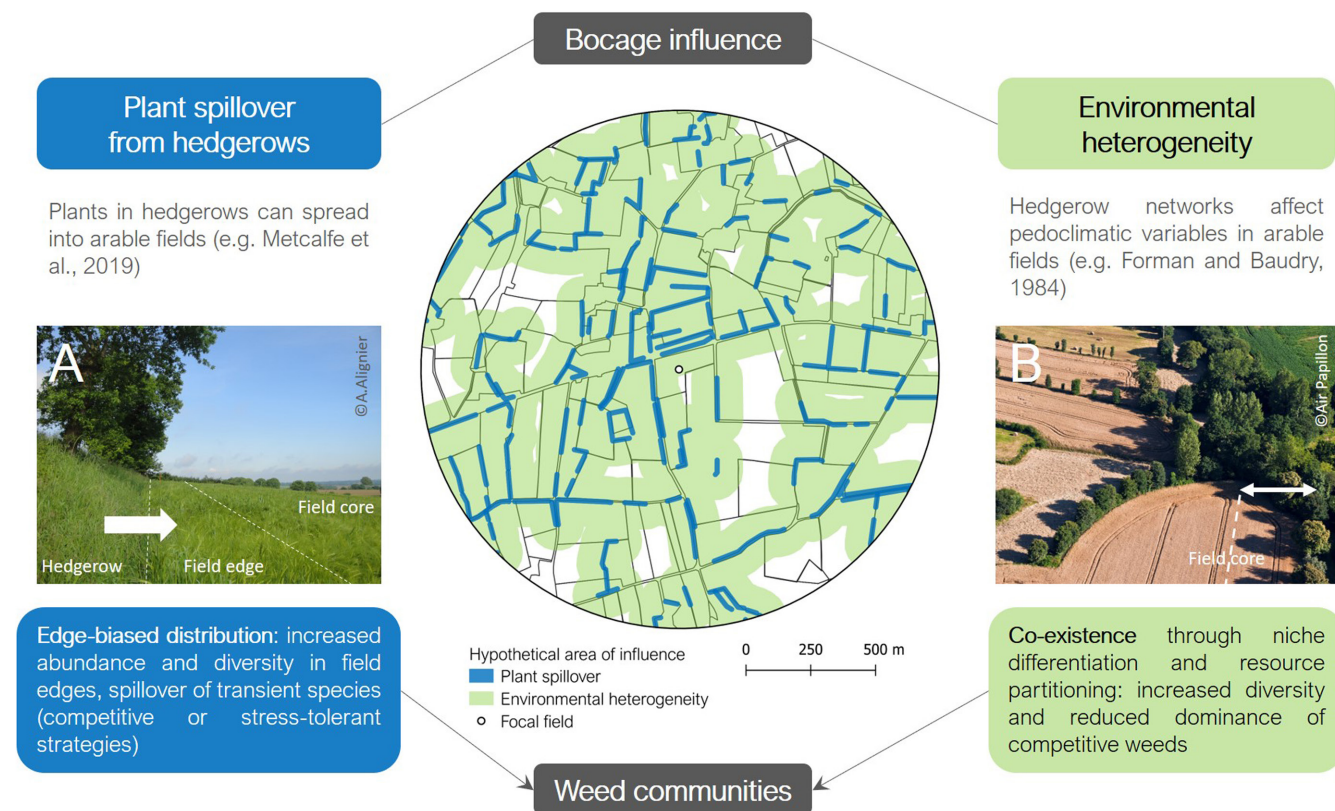
FIGURE 1 Dense and complex hedgerows networks (hereafter called 'bocage') could affect weed communities through two main processes. (a) Plant spillover from hedgerows increases weed cover and diversity, as well as the proportion of transient species with competitive or stress-tolerant strategies, within arable fields. (b) Dense and complex hedgerow networks lead to higher environmental heterogeneity in arable fields, in turn favouring weed diversity and reducing the dominance of competitive weeds through niche differentiation and resource partitioning. Very roughly, we represented the hypothetical area of influence of plant spillover (in blue) and environmental heterogeneity (in green) at the landscape scale, choosing a radius of 10 and 100 m around each hedgerow, respectively, based on previous references (Forman & Baudry, 1984; Metcalfe et al., 2019). The photographs were taken in the zone atelier Armorique, a long-term socio-ecological research (LTSER) site in Brittany (France).

strategies, allowing the co-existence of a diversity of life strategies in weed communities. The leaf-height-seed scheme proposed by Westoby (1998) is very useful to describe key aspects of plant ecological strategies in response to resource availability and disturbances. Specific leaf area (SLA) is related to fast versus slow growth strategies, corresponding to the resource availability axis of Grime's CSR scheme, opposing the competitive and ruderal strategies (high SLA) to the stress tolerance strategy (low SLA). Plant height and seed mass reflect separate aspects of coping with disturbances and competition, corresponding to the opposition between competitive (high stature and large seeds) and stress-tolerant (short stature and large seeds) strategies on the one hand, and the ruderal strategy (short stature and small seeds) on the other hand. In addition, many studies showed that specific leaf area, plant height, and seed mass vary along environmental gradients of light, temperature, precipitations, soil moisture, and nutrient availability, as reviewed in Garnier et al. (2016). We evaluated the contribution of plant spillover and environmental heterogeneity to weed diversity in field cores. Under the 'plant spillover' hypothesis, 'bocage' should increase weed cover and diversity as well as the proportion of transient species with competitive or stress-tolerant strategies. On the other hand, under the 'environmental heterogeneity' hypothesis, 'bocage' should increase weed diversity, but not weed cover, while reducing the proportion of competitive weeds.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in the southern part of the Zone Atelier Armorique, a Long-Term Socio-Ecological Research (LTSER) site in Brittany, northwestern France (47°59′35N, 1°45′12W). This region is characterized by dense hedgerow networks and crop-livestock farming systems. Agricultural lands are dominated by wheat and maize fields and temporary grasslands, and dominant soil types are Brunisols and Luvisols (Figure 2). Hedgerows are mostly old (i.e. planted at least before World War II), and generally composed of oak *Quercus robur* or chestnut *Castanea sativa* trees planted on a bank and pruned for firewood every 9–12 years. When present, the shrub layer is generally dominated by hazel *Corylus avellana*, hawthorn *Crataegus monogyna*, blackthorn *Prunus spinosa*, spindle *Euonymus*
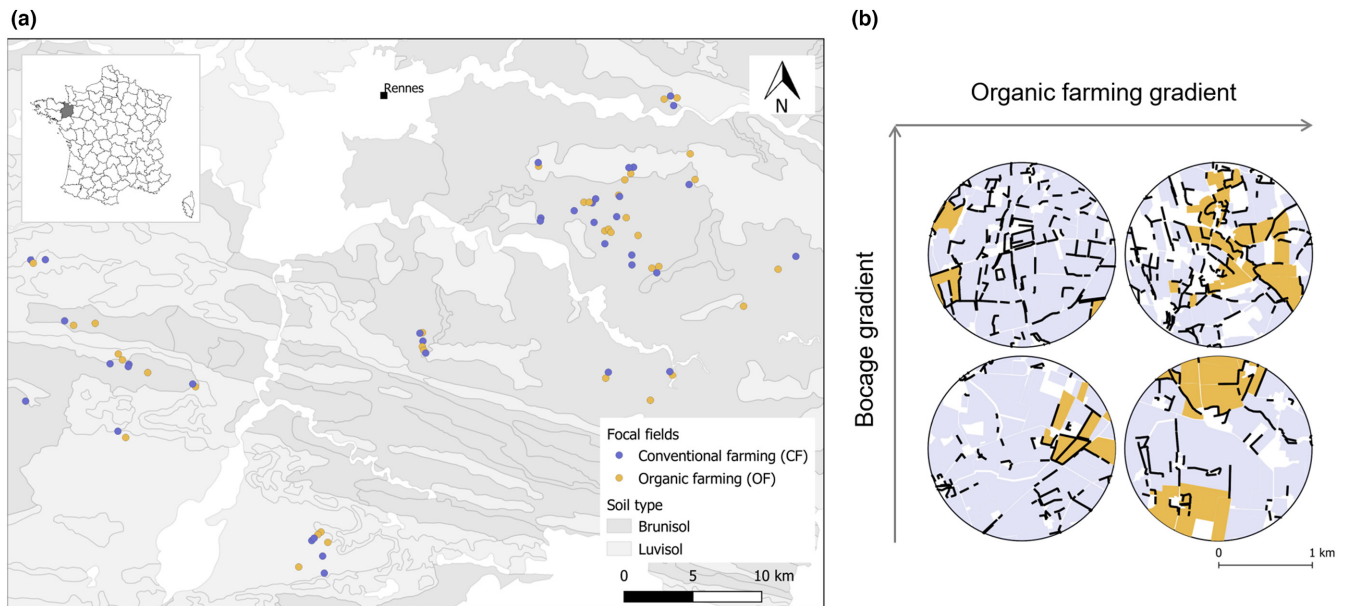
(a)

(b)

FIGURE 2 (a) Arable fields (*n* = 74) located in the southern part of the zone atelier Armorique, in Brittany (France). Soil map is provided by GéoSAS.fr (UMR SAS—INRAE—Institut agro Rennes Angers). (b) Fields are distributed along two independent landscape gradients of total length of hedgerows and organic farming cover. Blue and yellow areas represent conventional and organic farming systems, respectively.

europaeus, broom *Cytisus scoparius* or gorse *Ulex europaeus*. A more detailed description of hedgerow features in the study area, based on a sample of 40 hedgerows, is provided by Boinot and Alignier (2022). Photographs illustrating the diversity of hedgerows on our study site are provided in Figure S1.

Observation sites (*n* = 37) are located along two independent landscape gradients (*r* = 0.15, *p*-value = 0.20): total length of hedgerows (ranging from 6.3 to 18 km within a buffer radius of 1000 m around focal fields) and organic farming cover (ranging from 0% to 37% of total area within a buffer radius of 1000 m) (Figure 2). Each site contains a pair of fields less than 1 km apart and managed under conventional versus organic farming (CF vs. OF). Among these fields, 62 were grown with winter cereals, whereas 12 OF fields were grown with winter cereal-legume mixtures (we resorted to mixtures when we could not find any pure crop in the area). Management practices and landscape gradients were similar between pure crops and mixtures under OF (Figure S2). All farmers gave us permission for fieldwork. The study did not require ethical approval.

2.2 | Taxonomic and functional structures of weed communities

For each field, weeds were sampled on ten 1 m² located in the field core, at least 20 m from the field margin (sampling designs for each data set are provided in Figure S3). We sampled 20 pairs of fields in 2019 and 17 pairs of fields in 2020, in June and July before crop harvest. Pairs of fields sampled in 2019 were different from those sampled in 2020, but evenly located along the same range of landscape gradients. We visually estimated the cover of each species

found in quadrats, with an accuracy of ±5%. Ten quadrats per field were necessary to obtain a fairly accurate estimate of weed diversity, as indicated by species accumulation curves (Figure S4). Thus, we calculated the mean cover (%) of each species over the 10 quadrats for each field. Then, we measured total weed cover (i.e., the cumulative cover of all species), and species diversity (Hill-Shannon index) for each field. Hill-Shannon diversity considers both the number of species within a community and their relative cover to calculate the mean rarity of species within a community (Roswell et al., 2021). There was no weed in two CF fields, which were therefore assigned the lowest possible diversity value (zero).

We described the functional structure of weed communities using the community-weighted mean (CWM) and community-weighted variance (CWV) (Garnier et al., 2016) of the three traits included in the leaf-height-seed scheme: specific leaf area (SLA), plant height and seed mass. For each trait, CWM was calculated as the mean of trait values t_i of the S species in each field, weighted by the relative abundance of each species p_i:

$$CWM = \sum_{i=1}^{S} p_i \times t_i.$$

Then, CWV was computed as follows:

$$CWV = \sum_{i=1}^{S} p_i \times (t_i - CWM)^2.$$

Mean trait values for each species were collected in Ecoflora (Fitter & Peat, 1994) and LEDA (Kleyer et al., 2008) databases. Species with known trait values always represented more than 90% of the total weed cover for each field, thereby providing sufficient representativeness.

2.3 | Indicators of plant spillover and environmental heterogeneity

To estimate plant spillover, we used the phi coefficient of association, which distinguishes 'transient' species that rely on regular recolonization from neighbouring non-crop habitats, from 'resident' species typical of arable habitats and buffered by persistent seed-banks (Metcalfe et al., 2019). To avoid circular analysis, we used data from vegetation surveys at national scale. Weed frequency in arable fields was obtained from the 'Biovigilance Flore' network 2002–2012 (Fried et al., 2008), whereas plant frequency in uncropped field margins came from the '500 ENI' network (Fried et al., 2018). The fidelity score was calculated as follows, where $N = 7257$, the total number of plots (including arable fields and uncropped field margins), $N_p = 1875$, the number of plots in the habitat of interest (uncropped field margins), n is the total number of plots in which the species is found, and n_p is the number of plots where the species is found in the habitat of interest:

$$\text{Fidelity} = \frac{N \cdot n_p - n \cdot N_p}{\sqrt{n \cdot N_p \cdot (N - n) \cdot (N - N_p)}}.$$

Fidelity scores range from −1 to +1 with positive values indicating that the species and the habitat of interest co-occur more frequently than would be expected by chance. Larger values indicate a greater degree of joint fidelity. For each field, we computed the CWM and CWV of fidelity to estimate the contribution of spillover to plant diversity in arable fields. An increase in CWM Fidelity indicates greater spillover of transient species from neighbouring non-crop habitats. Further, an increase or a decrease in CWV Fidelity indicates co-existence or selection of fidelity values, respectively. Species with known fidelity values always represented more than 90% of the total weed cover, except for one field that was therefore excluded from analyses.

To estimate environmental heterogeneity within arable fields, we used CWM and CWV of Ellenberg indicator values for temperature (EIV-T), soil moisture (EIV-F), light (EIV-L), and nutrients (EIV-N). An increase in CWV values indicates higher environmental heterogeneity. Further, a shift in CWM values suggests a change in mean environmental conditions. Ellenberg values were collected in the Baseflor database (Julve, 1998). Species with known Ellenberg values always represented more than 90% of the total weed cover for each field. Correlations between traits values, Ellenberg values and fidelity scores were lower than 0.4 (Figure S5). Generalized pairs plots of response variables are given in Figures S6 and S7.

2.4 | Environmental factors

Kermap (https://kermap.com/en/) generated hedgerow mapping, using Computer Assisted Photo-interpretation based on the IGN orthophotograph of 2017. We rasterized vector maps with a resolution of one pixel for 5 m × 5 m to compute the 'bocage' metric, i.e., the density and complexity of hedgerow networks, within circular buffer radii of 250, 500, 750 and 1000 m around each field, using Chloe software (Boussard & Baudry, 2017). These buffer sizes correspond to the weed dispersal distances usually reported in the literature (e.g. Martin et al., 2020). 'Bocage' was calculated using the following formula based on landscape grain (Burel & Baudry, 1990), where n is the total number of pixels in a buffer zone and distance$_i$ is the distance from the pixel i to the nearest hedgerow:

$$\text{Bocage} = 1 - \frac{\sum_{i=1}^{n} \left(\min \left(\text{distance}_i, 100 \right) \right)}{n \times 100}.$$

Assuming that hedgerows are on average about 10 m high in the region (Boinot & Alignier, 2022), this index is based on the hypothesis that hedgerows located more than 100 m from a pixel have no or very little influence on it (Forman & Baudry, 1984). 'Bocage' varies from 0 to 1, with values close to 1 indicating a dense hedgerow network with a complex spatial configuration. We did not find strong correlations between 'bocage' and other metrics known to affect weed diversity, such as focal field size, percentage of semi-natural habitats (excluding hedgerows), or crop diversity in the landscape ($|r| < 0.36$; Figures S8–S11).

We assessed the effects of local farming systems (CF vs. OF). OF systems were characterized by the absence of herbicide treatment, lower N-fertilization but higher soil disturbances in our study site (Figures S12 and S13). We considered both organic and mineral fertilization, converting organic fertilization into nitrogen amounts per hectare. Maize—winter wheat is by far the most common crop rotation in CF systems, whereas OF systems generally have more complex crop rotations, including polycultures and temporary grasslands. On average, surveyed fields have been under OF for 23 ± 6 years. Finally, we computed the total cover of OF systems (%OF) within circular buffer radii of 250, 500, 750, and 1000 m around each field, based on geographical data of CF versus OF systems in the Department of Ille-et-Vilaine in 2019 (provided by the CartoBio team of the French Agency for the Development and Promotion of Organic Agriculture).

2.5 | Data analysis

We used generalized additive models (GAMs) to assess the effect of 'bocage', farming system at field and landscape scales, and two-way interactions on weed communities in field cores ($n = 74$ fields). The spatial coordinates of each field were included in GAMs to account for spatial autocorrelation, thanks to a smooth term modelling the interaction between latitude and longitude (Fried et al., 2018). 'Year' was also included as a covariate. We computed Gamma GAMs for total weed cover, Hill-Shannon diversity, CWV indices, and CWM Seed mass, and Gaussian GAMs for other CWM indices, using the R package MGCV (Wood, 2017). We added a small constant (10^{-6}) to total weed cover and Hill-Shannon diversity to allow for 0 values in Gamma GAMs. For CWM SLA, CWM EIV-L, and CWV EIV-L, we removed one CF field with extreme value that was unduly influencing the results. All explanatory variables were standardized

(mean-centred and divided by two standard deviations) to compare their relative importance (Schielzeth, 2010). The degree of collinearity between explanatory variables was checked before data analyses using generalized pairs plots (Figures S14–S17) and variance inflation factors (VIF). All explanatory variables had VIF values lower than 3 and thus were included in full models (Zuur et al., 2013).

We proceeded to a model averaging procedure based on information-theoretic approach (Burnham et al., 2011), using the R package MuMIn (Barton, 2020). We used the 95% confidence model set (i.e. summed Akaike weights from largest to smallest until reaching 0.95) to delineate a top model set. We performed an analysis for each buffer scale separately.

3 | RESULTS

Across the 74 arable fields surveyed, we recorded a total of 125 weed species belonging to 28 families. Relative cover of top 10 families was in decreasing order: Poaceae (20%), Fabaceae (19%), Juncaceae (16%), Asteraceae (11%), Caryophyllaceae (4%), Primulaceae (4%), Plantaginaceae (4%), Papaveraceae (3%), Convolvulaceae (3%) and Rosaceae (3%). Top 10 most frequent species observed in arable fields were in decreasing order: *Juncus bufonius* (68%), *Lysimachia arvensis* (61%), *Poa annua* (59%), *Veronica arvensis* (58%), *Polygonum aviculare* (55%), *Trifolium repens* (51%), *Tripleurospermum inodorum* (45%), *Viola arvensis* (43%), *Convolvulus arvensis* (43%) and *Aphanes arvensis* (42%). More detailed information on species composition in conventional versus organic farming (CF vs. OF) is given in Figure S18.

3.1 | Effects of environmental factors on weed communities

'Bocage' and organic farming cover in the landscape (%OF) did not affect total weed cover in arable fields, whatever the buffer radius (Figure 3a and Figure S20). Total weed cover was higher in OF fields (60 ± 30% vs. 9 ± 14% for CF).

'Bocage' increased species diversity of weed communities, independent of farming systems at field and landscape scales, within a buffer radius of 250, 750, and 1000 m (Figure 3b and Figure S21). Higher %OF also tended to increase species diversity (Figure 3b and Figure S21). Species diversity was higher in OF fields (12 ± 5 vs. 4 ± 3 for CF) (Figure 3b and Figure S21).

'Bocage' affected both community-weighted mean (CWM) and variance (CWV) of functional traits in weed communities (Figure 3 and Figures S22–S27). 'Bocage' decreased CWM Plant height only within a buffer radius of 250 m (and almost significantly within a buffer radius of 500 m) (Figure S24). Further, 'bocage' increased CWV of SLA (Figure 3d and Figure S23), plant height (Figure 3f and Figure S25), and seed mass (Figure 3h and Figure S27), within a buffer radius of 750 and 1000 m. These effects were generally independent of farming systems at field and landscape scales, except

for CWV SLA, for which 'bocage' effects (from 500 to 1000 m) tended to be more pronounced in CF fields (Figure S23). %OF did not affect CWM and CWV of weed communities (Figure 3 and Figures S22–S27). CWV Seed mass increased in OF fields (Figure 3h and Figure S27).

3.2 | Assessment of the 'plant spillover' and 'environmental heterogeneity' hypotheses

Regarding the 'plant spillover' hypothesis, 'bocage' did not affect CWM Fidelity, whatever the buffer radius (Figure 4a and Figure S28). On the other hand, CWM Fidelity was higher in OF fields and tended to increase with higher %OF in the landscape (Figure 4a and Figure S28). In addition, CWV Fidelity was higher in OF fields, and there was a negative interaction between 'bocage' and OF within a buffer radius of 750 and 1000 m (Figure 4b and Figure S29).

Regarding the 'environmental heterogeneity' hypothesis, 'bocage' increased CWV of Ellenberg values for temperature (EIV-T), soil moisture (EIV-F), and light (EIV-L) at multiple buffer scales (Figure 5, Figures S31, S33 and S35). 'Bocage' also increased CWV of Ellenberg values for nutrients (EIV-N) within a buffer radius of 1000 m (Figure S37), and almost significantly within a buffer radius of 750 m (Figure 5h). CWV EIV-T and CWV EIV-L were also higher in OF fields (Figure 5b,f). %OF did not affect CWV of Ellenberg values (Figure 5, Figures S31, S33, S35 and S37). In contrast to CWV, CWM of Ellenberg values were generally less influenced by the environmental factors and results were not consistent across buffer scales (Figure 5, Figures S30, S32, S34 and S36). Nonetheless, 'bocage' decreased CWM EIV-N within a buffer radius of 250 m and 500 m, whereas there was a negative interaction between 'bocage' and OF within a buffer radius of 750 and 1000 m (Figure 5g and Figure S36).

4 | DISCUSSION

4.1 | Weed communities are more diverse, but not more abundant, in dense and complex bocage landscapes

On the one hand, our results are consistent with those from Dainese et al. (2017), who found no effect of hedgerow density in the landscape on weed cover. Weed cover strongly depends on local practices rather than landscape context (Petit et al., 2016). Indeed, organic farming at field scale was the only variable affecting weed cover, with a strong positive effect due to the absence of herbicide treatments, as shown in many studies (e.g. Gabriel et al., 2010; Roschewitz et al., 2005). On the other hand, Dainese et al. (2017) found no effect of hedgerow density on weed species richness, whereas we found positive effects of 'bocage' on species diversity. Hedgerow densities, buffer scales, and dominant crop types were similar between the two studies. The difference in results could arise from different regional contexts (e.g. climate, management,
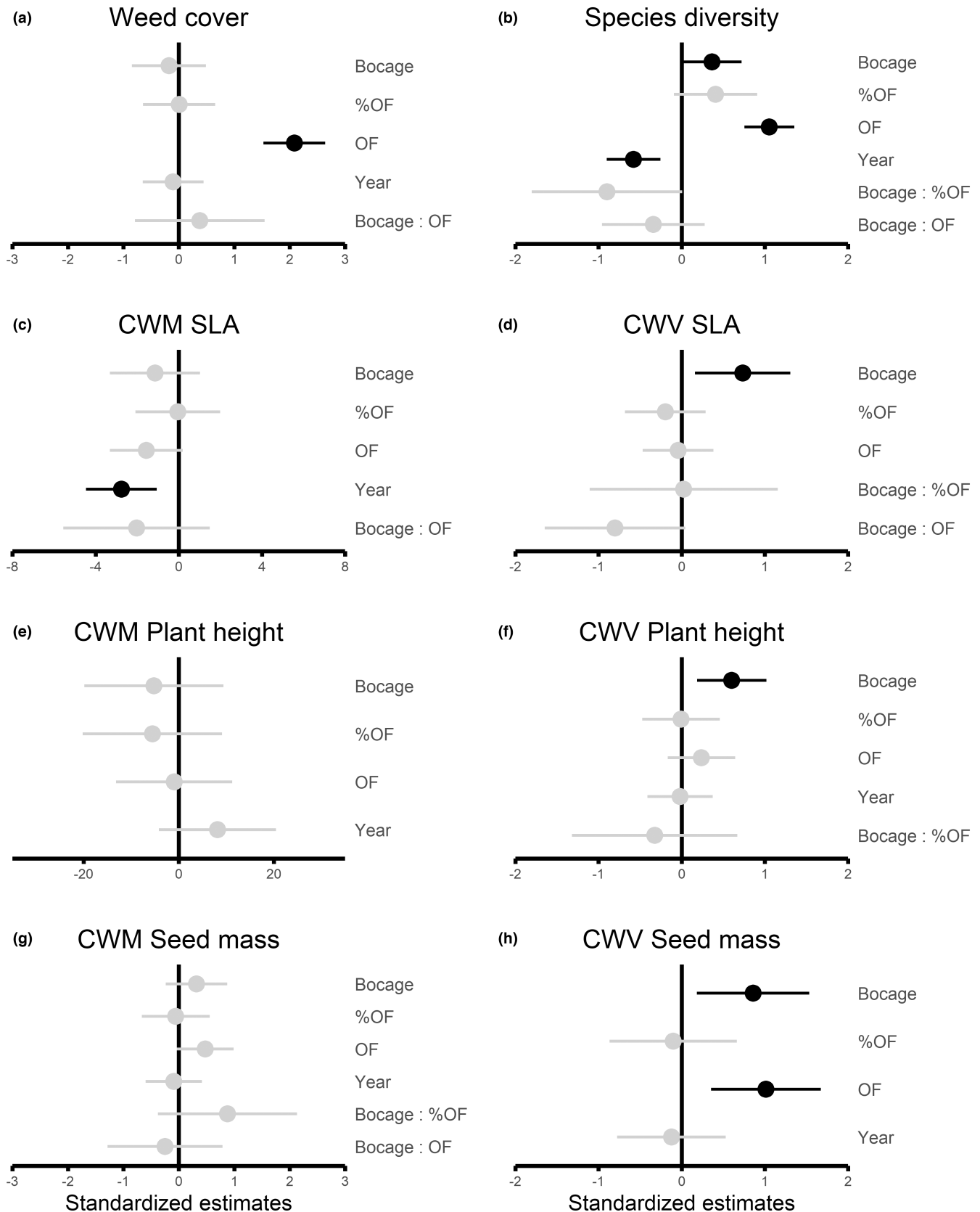
FIGURE 3 Standardized effects of environmental factors selected by the model averaging procedure on (a) total weed cover, (b) species diversity (Hill-Shannon index), (c) community-weighted mean (CWM) of specific leaf area (SLA), (d) community-weighted variance (CWV) of SLA, (e) CWM plant height, (f) CWV plant height, (g) CWM seed mass, and (h) CWV seed mass. We included two-way interactions between 'Bocage', organic farming cover in the landscape (%OF), and organic farming at field scale (OF). Significant effects are shown in black (i.e., zero does not fall within the 95% confidence interval). For plotting purposes, we only represent the results using a buffer radius of 750m, which was the most influential scale and provides a good summary of the most robust results (i.e. those observed at multiple buffer scales) (Figure S19). Full results are given in Figures S20–S27.

and history) or different hedgerow structures, compositions, and configurations (e.g. simple and single-storied hedgerows in north-eastern Italy vs. heterogeneous hedgerows in Brittany). The choice of diversity indices could also explain these contrasting results; Hill-Shannon diversity is based on the number of species but also on their relative cover, thus considering the interactions between species.

Surprisingly, we found that 'bocage', more than organic farming at field scale, enhanced weed functional diversity, despite the stronger effects of organic farming on weed cover and species diversity. In line with previous studies, we found that weed species diversity tends to increase with higher organic farming cover in the landscape (Henckel et al., 2015; Petit et al., 2016), most likely due to weed spillover from organic fields. Yet, organic farming cover did not affect weed functional diversity, probably because species favoured by higher organic farming cover share similar functional attributes. On the other hand, 'bocage' increased CWV of SLA, plant height and seed mass. These results strongly suggest that increased environmental heterogeneity drives higher diversity of life strategies in dense and complex bocage landscapes. First, the increase in species and functional diversity of weeds was not associated with an increase in total weed cover, contrary to what

is expected under the 'plant spillover' hypothesis (e.g. Alignier et al., 2017; Metcalfe et al., 2019). Second, the increase in weed diversity was associated with a reduced dominance of competitive species as expected from niche differentiation and resource partitioning processes, whereas plant spillover from hedgerows would result in a higher proportion of competitive species (Metcalfe et al., 2019). Undoubtedly, agrochemical disturbances and simplified crop rotations are major selection pressures for weed communities, which could impact other functional traits (e.g. phenological traits) not considered in our study (e.g. Rotchés-Ribalta et al., 2020). Nonetheless, our results suggest that the environmental homogenization caused by the destruction of hedgerow networks also has a major impact, and largely restricts the diversity of plant life strategies.

4.2 | Weed diversity is driven by environmental heterogeneity more than plant spillover

Results on fidelity to non-crop habitats and Ellenberg values provide further support for the 'environmental heterogeneity' hypothesis.
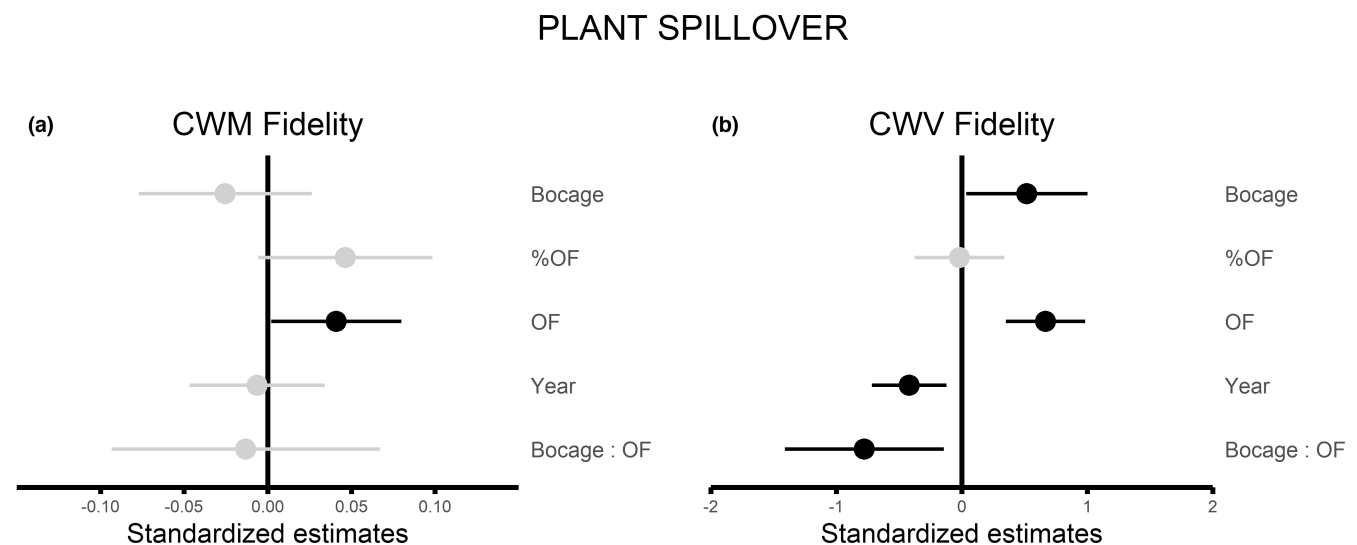

FIGURE 4 Assessment of the 'plant spillover' hypothesis. Standardized effects of environmental factors selected by the model averaging procedure on the indicators of spillover intensity: (a) community-weighted mean (CWM), and (b) community-weighted variance (CWV) of fidelity to non-crop habitats. We included two-way interactions between 'Bocage', organic farming cover in the landscape (%OF), and organic farming at field scale (OF). Significant effects are shown in black (i.e., zero does not fall within the 95% confidence interval). For plotting purposes, we only represent the results using a buffer radius of 750 m, which was the most influential scale and provides a good summary of the most robust results (i.e. those observed at multiple buffer scales) (Figure S19). Full results are given in Figures S28–S29.

FIGURE 5 Assessment of the 'environmental heterogeneity' hypothesis. Standardized effects of environmental factors selected by the model averaging procedure on the indicators of environmental heterogeneity: (a) community-weighted mean (CWM), and (b) community-weighted variance (CWV) of Ellenberg indicator value for temperature (EIV-T), (c) CWM and (d) CWV EIV-F (soil moisture), (e) CWM and (f) CWV EIV-L (light), (g) CWM and (h) CWV EIV-N (nutrients). We included two-way interactions between 'Bocage', organic farming cover in the landscape (%OF), and organic farming at field scale (OF). Significant effects are shown in black (i.e., zero does not fall within the 95% confidence interval). For plotting purposes, we only represent the results using a buffer radius of 750 m, which was the most influential scale and provides a good summary of the most robust results (i.e. those observed at multiple buffer scales) (Figure S19). Full results are given in Figures S30–S37.

ENVIRONMENTAL HETEROGENEITY
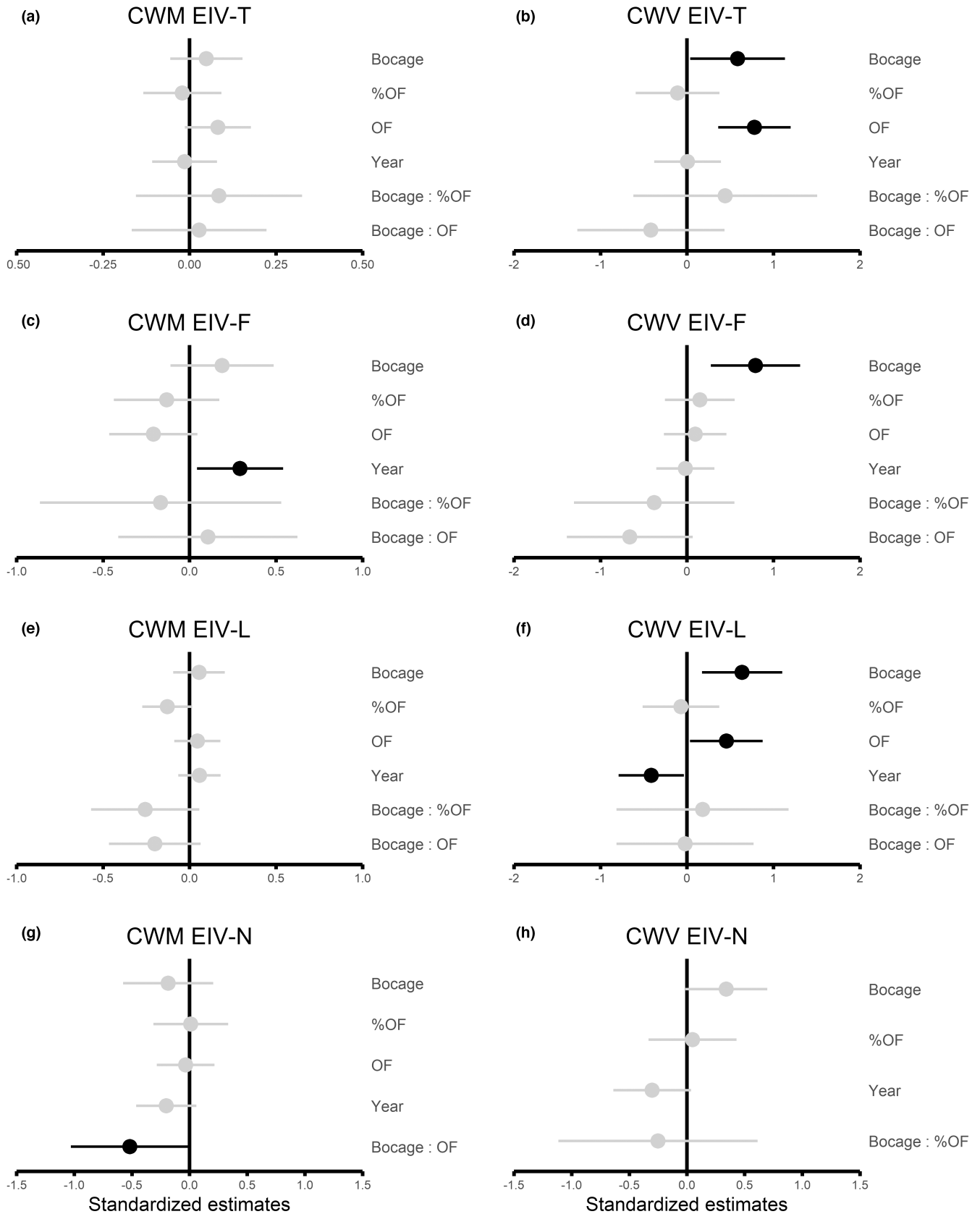
First, 'bocage' did not affect CWM of fidelity to non-crop habitats, indicating that spillover of transient species from hedgerows towards field cores (at more than 20 m from nearest hedgerows) is anecdotal or non-existent. This is in line with previous studies showing that detrimental spillover effects are generally restricted to the field edge, at least under conventional farming (e.g. Marshall, 1989; Metcalfe et al., 2019; Raatz et al., 2021). Fidelity to non-crop habitats increased in organic fields, but this was not due to increased density of hedgerows in the landscape. Increased fidelity to non-crop habitats in organic fields is probably due to presence of sown species used for cover crops and temporary grasslands (e.g. vetches and clovers). Additional transient species could also come from other semi-natural habitats such as grasslands or herbaceous field margins (Metcalfe et al., 2019). On the contrary, dense and undisturbed hedgerows could act as physical barriers preventing weed dispersal between fields, and as sink habitats with unfavourable pedoclimatic conditions for weed growth (e.g. lower resource availability, shade) (Wilkerson, 2014). Second, CWV of Ellenberg values for temperature, soil moisture, light, and to a lesser extent nutrients, increased in dense and complex bocage landscapes, suggesting an increase in environmental heterogeneity. These pedoclimatic parameters could play a preponderant role in weed community assembly and co-existence. For instance, García De León et al. (2014) demonstrated that changes in spring temperature can shift the competitive balance between weed species, depending on their ecological preferences and relative growth rates. Competition for light is also a key determinant of weed community assembly (Perronne et al., 2014). Besides, Silvertown et al. (1999) revealed that fine-scale variation in soil moisture allows for niche differentiation and co-existence in meadow plant communities. This could hold for weed communities, but studies considering fine-scale environmental heterogeneity are lacking.

Beyond abiotic factors, dense and complex bocage landscapes could also enhance biotic heterogeneity in arable fields, in turn favouring weed diversity, which requires further investigation. For instance, hedgerows can promote pollinators (Morandin & Kremen, 2013), seed dispersers (Heath et al., 2017), and seed predators (Badenhausser et al., 2020) in agricultural landscapes, which can all affect weed communities and promote a diversity of life strategies (Fontaine et al., 2006; Hulme, 1998; Ozinga et al., 2009).

4.3 | Bocage effects are independent of farming systems at field and landscape scales

Contrary to our expectations, 'bocage' effects were independent of farming systems at field and landscape scales. There were no synergetic effects between 'bocage' and organic farming systems, despite the absence of agrochemical disturbances in organic fields (Metcalfe et al., 2019). Alternatively, we assumed 'bocage' effects could be reduced in organic farming systems, which can reach carrying capacity even in intensive landscapes (Roschewitz et al., 2005), but this was not the case either. Through a meta-analysis, Seiferling

et al. (2014) revealed that an increase in environmental heterogeneity is particularly beneficial for biodiversity in highly disturbed and homogenized ecosystems. On the other hand, increasing environmental heterogeneity is more likely to have no effect on biodiversity, or even adverse effects, in more natural and heterogeneous ecosystems. Arable fields are highly disturbed ecosystems, even when managed organically, due to tillage operations and annual crop rotations. In such disturbed and homogenized ecosystems, an addition of environmental heterogeneity increases resource opportunities in a similar way (regardless of the farming system). This promotes niche partitioning and species coexistence, provided that there are indeed species with adequate life strategies to take advantage of these opportunities. However, of the two conventional fields where no weeds could be found, one was located in well-preserved bocage landscapes, highlighting that environmental heterogeneity cannot promote diversity if weed control is too strong.

4.4 | Management strategies to take full advantage of bocage landscapes

Farmers are often concerned that hedgerows harbour competitive weeds spreading into arable fields, and sometimes spray herbicides directly at the base of the hedge to prevent herbaceous flora from growing. However, we found that dense and complex bocage landscapes increased both species and functional diversity, reduced the dominance of competitive weeds, and did not increase weed cover in field cores. Therefore, weed communities of dense and complex bocage landscapes probably provide a wider range of trophic and microhabitat resources for farmland biodiversity (Gardarin et al., 2018), while causing lower yield losses through competition (Storkey & Neve, 2018). These beneficial effects of hedgerows on weed communities provide an additional argument for the reintroduction of trees and shrubs in agricultural landscapes, which deliver many ecosystem services including biodiversity conservation, sustainable food and biomass production, soil and water protection, and carbon sequestration.

An exciting avenue for research on bocage landscapes is the description of hedgerow quality at landscape scale, which could improve our understanding of the role of bocage on biodiversity conservation and agricultural production. Hedgerows that have survived agricultural intensification are being degraded in Brittany, through inappropriate management or neglect (Alignier & Baudry, 2015), like in many other European regions (Deckers et al., 2004; Litza & Diekmann, 2017; Tilzey, 2021). Hedgerows that lose structure and density have less impact on field microclimate, which probably undermines the beneficial effects of hedgerows on weed communities, as well as many other functions (e.g., provision of food and habitats for biodiversity, soil and water protection, crop and livestock protection, carbon sequestration). Management practices that preserve the structure and functionality of hedgerows include coppicing or hedge-laying, reduction of flailing frequency, preservation of tall trees with large canopies at frequent intervals,

and protection from both browsing by domestic animals and agro-chemical drifts (Tilzey, 2021). Following these guidelines, a network of well-preserved hedgerows in the landscape should favour agro-ecological weed management and biodiversity conservation.

CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.k0p2ngfbv (Boinot et al., 2022).

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