

A functional diversity approach of crop sequences reveals that weed diversity and abundance show different responses to environmental variability

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Funding information

Fondation pour la Recherche sur la Biodiversité; Agence Nationale de la Recherche, Grant/Award Number: ANR-13-AGRO-0001

Handling Editor: David Moreno Mateos

Abstract

1. Combining several crop species and associated agricultural practices in a crop sequence has the potential to control weed abundance while promoting weed diversity in arable fields. However, how the variability in environmental conditions that arise from crop sequences affects weed diversity and abundance remains poorly understood, with most studies to-date simply opposing weed communities in monoculture and in crop rotation. Here, we describe crop sequences along gradients of disturbance and resource variability using a crop functional trait and associated agricultural practices. We tested the hypothesis that in disturbances reduces weed abundance, whereas variability in resources promotes weed diversity.
2. We used functional Hill's numbers to compute crop sequence functional diversity based on sowing date, herbicide spectrum and crop height—these are the respective proxies of disturbance timings, disturbance types and light availability. Using a large-scale weed monitoring database, we assessed crop sequence diversity for 1,045 crop sequences of five consecutive cropping seasons. We computed weed richness and abundance at pluri-annual (pool of weeds observed across five cropping seasons) and annual (pool of weeds observed during a winter cereal cropping season preceded by five cropping seasons) scales. We also accounted for herbicide and tillage intensities to test whether management intensity affects the response of weed diversity and abundance to crop sequence diversity.
3. At the pluri-annual scale, weed richness increased with the diversity of crop height and sowing date, whereas weed abundance decreased with sowing date diversity. Annual weed richness decreased with sowing date diversity, whereas annual weed abundance poorly relied on crop sequence diversity.
4. *Synthesis and applications.* This study establishes a scientific basis for designing crop sequences according to specific weed management goals. We show that farmers may enhance arable weed diversity on a pluri-annual scale by sequentially sowing crop species that differ in their competitive ability and sowing date. They may also achieve a better control of weed abundance by increasing the diversity of crop sowing dates across the crop sequence.

KEYWORDS

agroecology, crop rotation, crop sequences, disturbance, functional diversity, Hill's number, resource availability, weed management

1 | INTRODUCTION

Crop sequences, the diversification of cropping systems in time, is a promising strategy for sustainable management in agriculture. Compared to monocultures, crop sequences optimize soil health and nutrient use and prevent the development of pests and disease specialists of a crop species (Curl, 1963; Dias, Dukes, & Antunes, 2015). More particularly, crop sequences provide a better control of weed abundance than monocultures (Koocheki, Nassiri, Alimoradi, & Ghorbani, 2009; Liebman & Dyck, 1993; Ruisi et al., 2015) and can promote weed diversity in arable fields (Murphy, Clements, Belaousof, Kevan, & Swanton, 2006; Ruisi et al., 2015; Ulber, Steinmann, Klimek, & Isselstein, 2009; but see Smith & Gross, 2007). Consequently, the establishment of diverse crop sequences has the potential to reduce the use of herbicides in arable fields (Westerman et al., 2005) and to contribute to biodiversity conservation in farmland (Marshall et al., 2003; Nicholls & Altieri, 2013). However, despite being a keystone direction of sustainable weed management, how to design crop sequences for a specific weed management goal (e.g. controlling weed abundance; promoting weed diversity) is surprisingly unclear. Indeed, most studies have investigated crop sequence effects on weed diversity and abundance by opposing monocultures with diversified crop sequences (e.g. Andrade, Satorre, Ermácora, & Poggio, 2017; Doucet, Weaver, Hamill, & Zhang, 1999; Koocheki et al., 2009; Murphy et al., 2006; Ruisi et al., 2015; Smith & Gross, 2007; Teasdale, Mirsky, & Cavigelli, 2018; Ulber et al., 2009). However, identities of crop species and their associated agricultural practices could generate various patterns of temporal variability in environmental conditions. For example winter barley cropped after winter wheat will generate lower environmental variability than a soybean cropped after a winter wheat. Therefore, if farmers wish to rationalize the use of crop sequences as an alternative weed management process, a better understanding of how the environmental variability that arise from crop sequences affects weed diversity and abundance is required.

During a cropping season (i.e. from sowing to harvest), crop species and associated farming practices dictate the types and timings of disturbances (mainly tillage and herbicide applications) as well as the amount of available resources for weeds (Gaba, Fried, Kazakou, Chauvel, & Navas, 2014). The latter is strongly correlated with the crop competitive ability to uptake resources (Gaba et al., 2014), notably light which is the main limiting resources for weeds (Weiner, Andersen, Wille, Griepentrog, & Olsen, 2010). Consequently, according to the identities of sequentially cultivated crops, crop sequences vary along gradients of disturbance and resources availability.

Greater variability in the types and timings of disturbances reduces population density and thus increases the risk of local stochastic extinction (Boyce, 1992). In contrast, temporal variability in resources availability promotes long-term species coexistence by preventing competitive exclusion from a dominant species (Chesson, 2000). Hence, weed abundance and diversity should decrease with the variability in disturbances, whereas weed diversity should increase with the variability in resources availability. However, assessing the effects of crop sequence diversity on weeds is not straightforward. Indeed, the great majority of arable weed species are annuals producing seeds that accumulate in a seed bank. On one hand, the pool of species in the seed bank (i.e. *pluri-annual species pool*; Figure 1) reflects environmental conditions that prevailed in the preceding cropping seasons (Bohan et al., 2011; Ryan, Smith, Mirsky, Mortensen, & Seidel, 2010). On the other hand, both temporal dispersal from the seed bank and contemporary environmental conditions (mainly disturbance timings) shape emerged weed communities during a given cropping season (i.e. the *annual species pool*; Figure 1). Since contemporary environmental conditions exert a stronger influence on the emerged weed community than temporal dispersal (Mahaut, Fried, & Gaba, 2018), the effects of crop sequence diversity on weed diversity and abundance should be stronger at the pluri-annual scale compare to the annual one. Moreover, there should be a greater influence of weed temporal dispersal on annual species pools at the beginning of a cropping season when competitive interactions among weed species and crop are weaker (Mahaut et al., 2018). Herbicides applications during a specific cropping season can also buffer the effects of weed temporal dispersal by the non-random selection of tolerant weed species to the spectrum of herbicides of the contemporary crop (Ulber et al., 2009). Consequently, the effects of crop sequence diversity on annual weed species pools should be stronger at the beginning of a cropping season, due to the low competitive intensity, and in the absence of contemporary herbicide application. Finally, if the effects of crop sequence diversity on weed diversity and abundance mostly rely on the diversity of disturbance types and timings, then decreasing disturbance intensity across a crop sequence—that is decreasing tillage and/or herbicide intensities—can reduce the influence of crop sequence diversity on weed diversity and abundance (Doucet et al., 1999).

Here, we developed a novel approach to characterize crop sequence diversity in a way that reflects the environmental variability that arises from various crop sequences. On the basis of a key functional trait of crop species and on two crop-associated farming practices related to disturbances and resources, we computed crop sequence functional diversity for 1,045 5-year crop sequences, using

the French national scale weed monitoring programme Biovigilance Flore (Fried, Norton, & Reboud, 2008). Then, we investigated how diversity of disturbance types and timings and diversity of resources availability affected weed diversity and abundance, with both being computed at pluri-annual and annual scales. We tested the general prediction that weed diversity and abundance decrease with higher diversity in disturbance types and timings, and that weed diversity increases with higher diversity in resources availability. We also tested the prediction that the effects of crop sequence diversity on the pluri-annual species pool are stronger than on annual species pools, and that these effects on annual species pools are stronger at the beginning of a cropping season and in the absence of herbicide application during the cropping season. Finally, we predicted stronger effects of the diversity of disturbance types and timings in fields where tillage and herbicide intensities were high.

2 | MATERIALS AND METHODS

2.1 | Dataset

We used data from the French monitoring programme Biovigilance Flore in which 1,440 fields were monitored across France between 2002 and 2010. The fields were selected to represent the diversity of farming practices and environmental conditions, covering 20 major crop species (Fried et al., 2008). Crop, herbicides and soil tillage were recorded each cropping season. Weeds were surveyed twice a year in a 2,000 m² plot subject to contemporary management practices (sprayed plots) and in a ~140 m² plot with the same practices, but excluding herbicides (control plots) by two trained

persons recording all species observed until no more new species were found. The first survey (T1) was carried out 1 month after sowing the crop, before post-emergence herbicide treatment. The second survey (T2) was carried out after the last herbicide treatment. Species densities were recorded using a semi-quantitative scale that we transformed into a quantitative scale using the median of each class of abundance, these classes representing 0.0005, 0.1, 1.5, 3.0, 11.5, 35.5 and 75.0 plants/m² respectively. We selected 473 fields where farming practices were recorded during at least five consecutive cropping seasons. This represented 1,045 crop sequences of five consecutive cropping seasons (i.e. fields that have been monitored more than five consecutive years were represented by several crop sequences in the selected dataset) and 81% of the 348 species recorded in Biovigilance Flore.

2.2 | Crop sequence functional diversity

We decomposed crop sequences into disturbance and resources gradients. Disturbance gradients were based on the diversity of both crop sowing date—a proxy of disturbance timings during a cropping season—and herbicides spectrum, which reflects the identities of weeds that are targeted by the herbicides' active ingredients (Gaba et al., 2014). Crop sowing dates were extracted from Biovigilance Flore dataset as Julian day of sowing. Herbicide spectrums were characterized using the Herbicides Resistance Action Committee (HRAC) classification (<http://hracglobal.com/tools/classification-lookup> visited on August 2015) which groups herbicide active ingredients according to their site(s) of action (Table S2). Resources gradient was based on the diversity of crop height, a proxy of

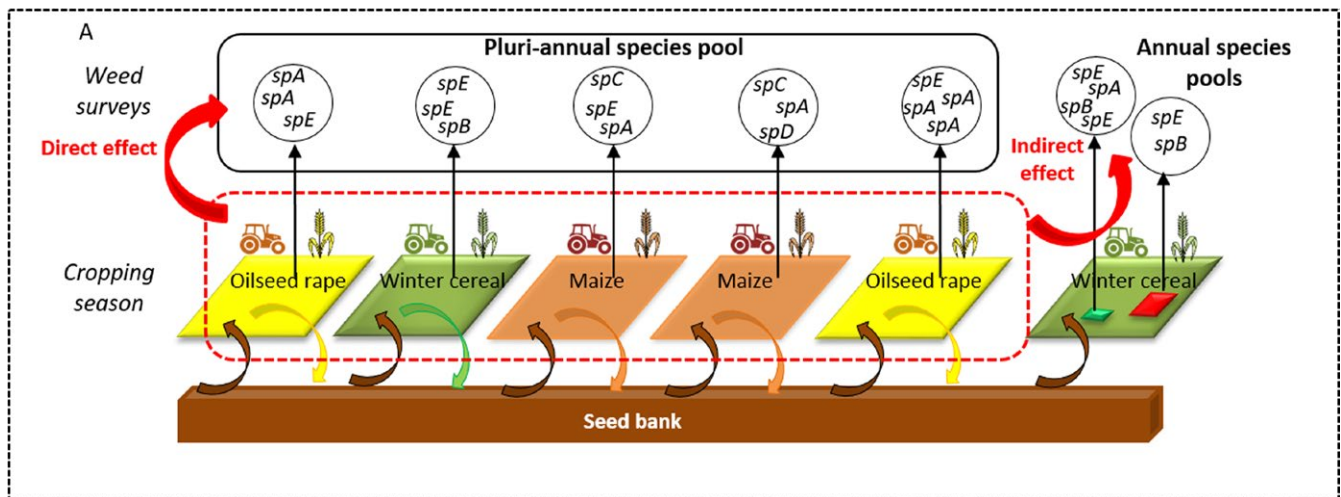


FIGURE 1 Schematic representation of a crop sequence that consists in six annual crops: oilseed rape, winter cereal, maize, maize, oilseed rape and winter cereal. Each cropping season, crop identity partly determines the type and timing of disturbances (coloured tractor) and the amount of available resources for weeds (coloured plant). These crop characteristics partly drive the assembly of weed community (open black circles) during a cropping season. Temporal variability in disturbances and resources availability arising from a crop sequence should therefore affect the diversity and abundance of the pool of weeds observed across consecutive cropping seasons (i.e. pluri-annual species pools). Yet, weed community assembly during a cropping also relies on the emergence of dormant seeds stored in the seed bank (brown arrows). Consequently, temporal variability in disturbances and resources availability may affect the diversity and abundance of the annual weeds species pools (i.e. pool of weeds observed during the latest cropping season), both in control plot (green) and in herbicide sprayed plots (red)

available light for weeds (Gaba et al., 2014; Gunton, Petit, & Gaba, 2011). Typical crop height was extracted from Gunton et al. (2011) (see Table S1).

We used functional Hill's numbers to compute the functional diversity of each 5-year crop sequence (Chao, Chiu, & Jost, 2014). Functional Hill's numbers reflect the effective number of species (here cropping season) among a delimited pool of species (here a 5-year crop sequence) given species functional dissimilarity (here based on a crop trait and two crop-associated farming practices). We computed the dissimilarity in disturbance types as the Jaccard dissimilarity index of herbicides HRAC classes between each pair of cropping seasons using the *vegdist* function in R *vegan* library. Dissimilarity in disturbance timings and in resources availability were computed as the Euclidian distance between the sowing dates and the crop height each of cropping season respectively (see Figure S1).

2.3 | Management intensity

Management intensity across crop sequences was assessed in terms of herbicide and tillage intensities. The intensity of herbicide applications was computed as the Treatment-Frequency Index (TFI), being the sum of the ratio of the applied dose to the recommended doses of all the herbicides applied during a cropping season. Tillage intensity was quantified based on the tillage system being either "conventional" for mouldboard ploughing, where seeds from the previous season were buried (inversion tillage), or "minimum" for no-till or reduced tillage, where previously produced seeds were not buried. Management intensity was approximated using the average TFI herbicide and the total number of mouldboard ploughing over the crop sequence.

2.4 | Weed diversity and abundance

We computed weed diversity and abundance in annual and pluri-annual weed species pools. To account for the confounding effects of contemporary crop types, annual species pool was delineated as all weed species surveyed in the field over a winter cereal cropping season (the most representative crop type in our dataset; Table S1) preceding by a 5-year crop sequence (Figure 1). Annual weed richness and abundance, calculated as the sum of species annual class of abundance, were computed separately in 255 T1 control plots, 230 T2 control plots and 208 T2 sprayed plots corresponding to 188, 169 and 159 arable fields respectively (Figure S2). Pluri-annual species pool was delineated as all weed species surveyed over five consecutive cropping seasons (Figure 1). To encompass the total number of recorded species, we built pluri-annual species pools using weed surveys in control and herbicide-sprayed plots, conducted at the beginning (T1) and at the middle (T2) of the cropping season. For each recorded species, we conserved its maximal class of abundance and computed pluri-annual abundance as the sum of species maximal class of abundance. Data for pluri-annual species pool were available for 295 crop sequences corresponding to 168 distinct arable fields (Figure S2).

2.5 | Analysis

We investigated the influence of crop sequence diversity and management intensity on weed communities using generalized linear models (GLM) with a Poisson distribution and log link functions for weed richness and linear models (LM) for weed abundance. Models were run separately for pluri-annual species pools and annual species pools in T1 control, T2 control and T2 sprayed plots. Pluri-annual weed species pool abundance was square-root transformed and abundance of annual weed species pools was log transformed to satisfy the normality assumption.

We used an Akaike information criterion (AIC) multi-model selection framework (Garamszegi, 2011) to evaluate the extent to which the data supported four competing models of increasingly complexity using the *dredge* function of *MuMIn* R library (Bartoń, 2018). All retained covariates of the lower level models were included in the more complex models. Models in which the difference in AIC (ΔAIC) ≥ 2 were considered to have the best support.

The first model (M0 "baseline model") accounted for the confounding effects of soil pH and latitudinal and longitudinal gradients on weed diversity and abundance (Fried et al., 2008). This baseline model also accounted for the year of weed survey (i.e. 2007, 2008, 2009 or 2010) only in annual weed species pool models as annual climatic conditions can influence weed diversity and abundance (Fried et al., 2008). All retained covariates from this baseline model were added in the more complex models. Second, we tested separately for the effects of either management intensity (herbicide and tillage; M1a) or crop sequence diversity (diversity of disturbance timings, disturbance types and resources availability; M1b) on weed diversity and abundance, accounting for two-way interactions among management intensity (M1a) or crop sequence diversity variables (M1b). Finally, we investigated the interactive effect of management intensity and crop sequence diversity by building a model with all two-way interactions between management intensity and crop sequence diversity variables (M2). We did not include the interactions between biogeographical gradients and other covariates because they would have been hard to interpret, since both response and explanatory variables covary along these gradients. We standardized all variables and used the sum of the square of each explicative variable given by the ANOVA (*types III*) to evaluate their contribution.

As we had several 5-year crop sequences per field, we randomly selected one crop sequence per field to ensure for data independence. We generated 100 datasets of 168, 188, 169 and 159 crop sequences, respectively, for pluri-annual, annual T1 control, annual T2 control and annual T2 sprayed (with one crop sequence per field) and ran the model selection procedure described above (see Figure S2). The 100 repetitions allow checking for the robustness of the results. Results were highly homogeneous among the 100 datasets, except for the annual abundance in T2 sprayed plots (Table S3). Consequently, in the result section we present the selected model that has the highest goodness-of-fit (i.e. highest determination coefficient; r^2) among the 100 selected models for each species pool (Figure S2). Mean and standard deviations of the variables used in

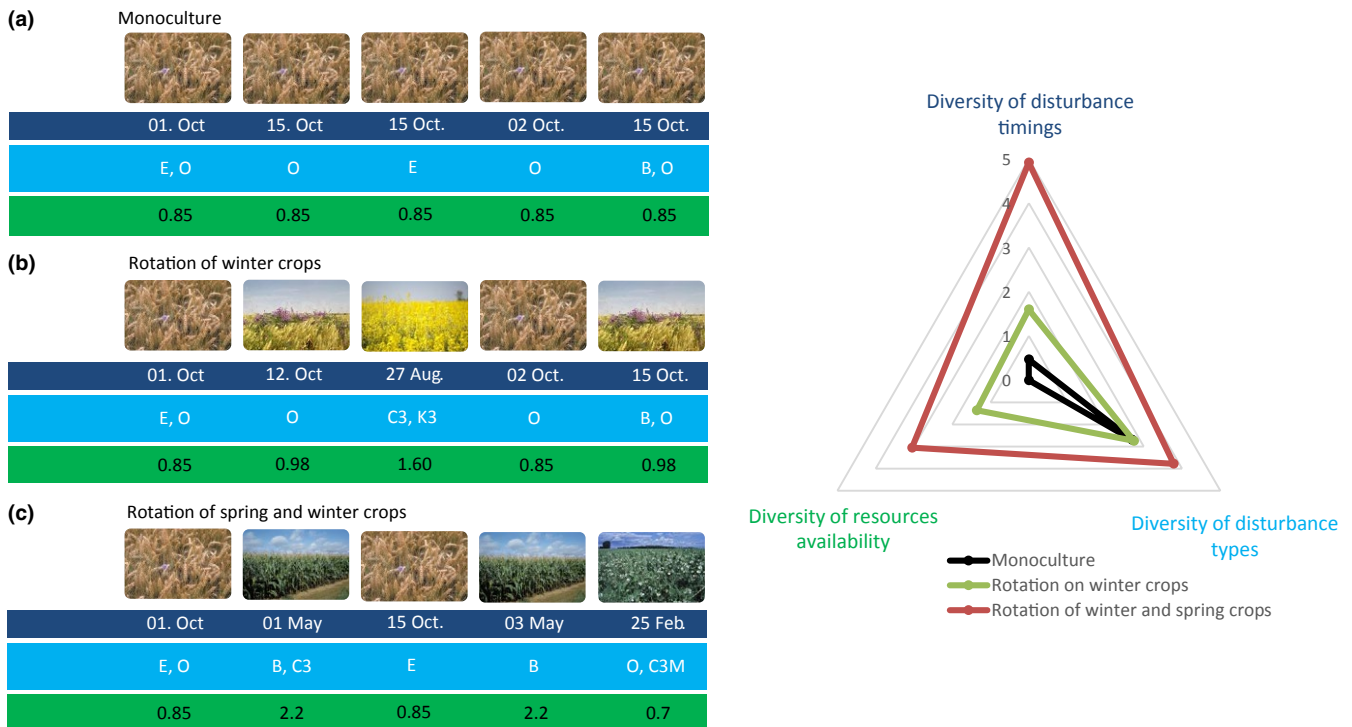


FIGURE 2 Left: Three crop sequences of increasing diversity. Disturbance variability arising from crop sequence is based on the diversity of sowing day (a proxy of disturbance timings) and herbicide HRAC classes (a proxy of disturbance types), whereas variability in resources availability is based on the diversity of crop height (a proxy of light availability). Monoculture (a) is a sequence made of a single-crop species (here a winter wheat) where sowing day and herbicide HRAC classes can slightly vary from year to year, according to farmer choice. Rotation of winter sown crops (b) corresponds to sequences that involve different crop species sown during the same season (here winter wheat, winter barley and oil seed rape), whereas rotation of spring and winter crops (c) corresponds to sequences made of crops that are sown at different seasons (here winter wheat, maize and spring pea). Right: Crop sequences continuously vary according to their diversity in disturbance timings, disturbance types and resources availability, which are computed through functional Hill's number (see Section 2 for more details)

these models are presented in Supporting Information (Tables S4 and S5).

Finally, because the different facets of crop sequence functional diversity were positively correlated (from 0.31 to 0.47, Figure S3), we tested for multi-collinearity by calculating the variance inflation factor (VIF), as it can significantly increase the variance of the parameter estimates (O'Brien, 2007). For a value of VIF less than 10, the collinearity is negligible. We did not find severe collinearity for any of the models (VIF < 5.07 in all cases). Analyses were conducted in R ver. 3.4.0 (<https://www.r-project.org/>).

3 | RESULTS

3.1 | Describing crop sequences along environmental gradients

Our approach, based on the functional diversity of crop sequence, was robust in sorting out crop sequences, from monoculture (Figure 2a) to sequences that differ in their resources availability (e.g. crop height, Figure 2b) or their timings and types of disturbance (e.g. sowing date and herbicides; Figure 2c). In monoculture, our approach detected a year-to-year variability in farming practices, as

revealed by the diversity of the timings and types of disturbance (Figure 2a). From the 1,045 5-year crop sequences in our dataset, the diversity of disturbance timings continuously varied from 0.06 (corresponding to crop sequences with quite similar days of sowing each cropping season), to 7.17 (i.e. crop sequences with crops sown at different seasons; Figure S1). The diversity of disturbance types varied from 0.392 (i.e. crop sequences in which herbicides applied each cropping season show similar HRAC classes) to 5.0 (i.e. crop sequences in which herbicides applied each cropping season had no HRAC classes in common; Figure S1). Lastly, the diversity of resources availability varied from 0.0 when the same crop is sown each year during the crop sequence to 4.0 in crop sequences where the crops all have different heights (Figure S1).

3.2 | Predictability of weed richness and abundance

For weed richness and abundance in pluri-annual and annual species pools, the model accounting for interactive effects between crop sequence diversity and management intensity (M2) had always the lowest AIC score, indicating that weed richness and abundance were determined by the combined effect of crop sequence diversity and management intensity (Table S6). According to the species pool, the

selected M2 models explained between 12% and 26% of the variance of weed richness (Figure 3a) and between 14% and 32% of the variance of weed abundance (Figure 3b).

3.3 | Effects on weed species richness

Globally, biogeographical gradients exerted the strongest influence on weed richness, followed by crop sequence diversity and then management intensity (Figure 3a). During a cropping season, the influence of both crop sequence diversity and management intensity on weed richness increased from the beginning (T1 control plots) to the middle (T2 control plots) of a cropping season (Figure 3a).

As predicted, pluri-annual richness increased with the diversity of resources availability (Table 1). However, contrary to our hypothesis, it also increased with the diversity of disturbance timings (Table 1). At the annual scale, species richness at the beginning of a cropping season (T1 control plots) decreased with the diversity of disturbance types (Table 1). At the middle of a cropping season (T2 control and T2 sprayed plots), weed richness decreased with the diversity of disturbance timings (Table 1). Annual weed richness in T2 control and T2 sprayed plots also increased with the diversity of resources availability and with the diversity of disturbance types respectively (Table 1). However, the effects of the diversity of disturbance timings and of resources availability on weed richness in T2 control plots cancelled each other, as revealed by their negative interaction (Table 1). Finally, weed richness in T1 control and T2 sprayed plots decreased with herbicide intensity (Table 1).

3.4 | Effects on weed abundance

At the pluri-annual scale, management intensity exerted the strongest influence on weed abundance, followed by biogeographical gradients and crop sequence diversity (Figure 3b). Pluri-annual weed abundance decreased when both tillage and herbicide intensities

were high (Table 2). Furthermore, it decreased with the diversity of disturbance timings but increased with the diversity of resources availability (Table 2). However, the diversity of disturbance types reduced the negative effect of disturbance timings diversity on the pluri-annual weed abundance, whereas it increased the positive effect of the diversity of resources availability (Table 2). At the annual scale in control plots, biogeographical gradients exerted the strongest influence on weed abundance followed by crop sequence diversity or management intensity for weed abundance in T1 control and in T2 control plots respectively (Figure 3b). Weed abundance in T1 control plots decreased with the diversity of resources availability, whereas weed abundance in T2 control plots decreased when both herbicide and tillage intensities over a crop sequence were high (Table 2). Finally, according to the repetitions of the model selection procedure, biogeographical gradients were the main drivers of weed abundance in T2 sprayed plots, M0 being selected most of the time (Table S3).

3.5 | Management intensity affected the effects of crop sequence diversity

As expected, we reported numerous interactions between crop sequence diversity and management intensity over a crop sequence (Figure 3a,b). All the significant interactions between management intensity and crop sequence diversity affecting weed richness relied on tillage intensity (Table 1). For example both pluri-annual and annual weed richness in T2 sprayed plots decreased with the diversity of disturbance types when tillage intensity was high, whereas tillage intensity strengthened the positive effect of disturbance timings diversity on annual weed richness in T1 control plots (Table 1). In contrast, pluri-annual weed abundance decreased with the diversity of disturbance types when herbicide intensity was high (Table 2). Mean herbicide intensity over a crop sequence also strengthened the negative effect of the diversity of resources availability on annual abundance in T1 control plots (Table 2).

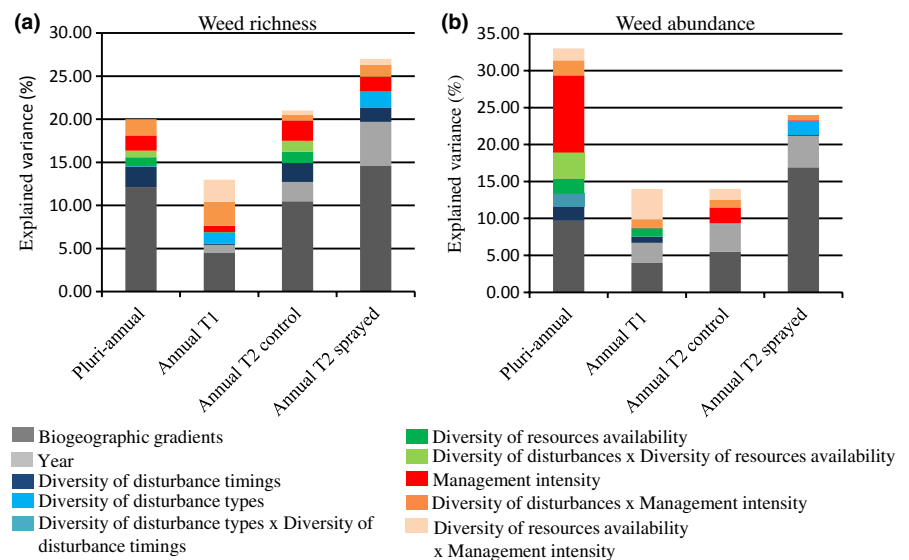


FIGURE 3 Percentage of explained variance by biogeographical gradients, year, diversity of disturbance timings and types, diversity of resources availability and management intensity over a crop sequence on weed richness (a) and abundance (b) in pluri-annual species pools and in annual species pools before herbicides application (T1) and after herbicides application (T2) in absence (control) or in presence of contemporary herbicide use (sprayed)

TABLE 1 Model outputs for weed richness (GLM) in pluri-annual species pool and annual species pools at the beginning of a cropping season (T1 control), at the middle (T2 control) and in herbicide sprayed plots

	Pluri-annual	Annual T1 control	Annual T2 control	Annual T2 sprayed
Biogeographical gradients				
Longitude	0.17 ± 0.01***	0.42 ± 0.07***	ns	ns
Latitude	-0.17 ± 0.03***	ns	-0.44 ± 0.06***	-0.69 ± 0.07***
Year 2008	-	-0.05 ± 0.10	0.15 ± 0.09	-0.05 ± 0.10
Year 2009	-	0.17 ± 0.11	0.25 ± 0.09**	0.20 ± 0.10*
Year 2010	-	0.08 ± 0.12	-0.03 ± 0.12	-0.55 ± 0.15***
Crop sequence diversity				
Resources availability	0.09 ± 0.04*	-0.05 ± 0.08	0.17 ± 0.07*	0.06 ± 0.08
Disturbance timings	0.15 ± 0.04***	0.07 ± 0.08	-0.26 ± 0.08**	-0.26 ± 0.08**
Disturbance types	0.02 ± 0.03	-0.23 ± 0.07**	ns	0.25 ± 0.08**
Resources availability × disturbance timings	ns	ns	-0.33 ± 0.14*	ns
Resources availability × disturbance types	0.11 ± 0.06*	ns	ns	ns
Management intensity				
Herbicide	-0.05 ± 0.03	-0.17 ± 0.08*	0.03 ± 0.06	-0.22 ± 0.07**
Tillage	0.03 ± 0.03	-0.07 ± 0.07	-0.23 ± 0.07	-0.08 ± 0.08
Herbicide × tillage	-0.11 ± 0.07	ns	ns	ns
Crop sequence diversity × management intensity				
Resources availability × tillage	ns	-0.66 ± 0.16***	-0.21 ± 0.14	0.30 ± 0.15*
Resources availability × herbicide	ns	-0.24 ± 0.16	ns	ns
Disturbance timings × tillage	0.11 ± 0.07	0.57 ± 0.13***	ns	ns
Disturbance timings × herbicide	ns	ns	-0.26 ± 0.15	ns
Disturbance types × tillage	-0.18 ± 0.07**	ns	ns	-0.42 ± 0.14**

Notes. Estimates are qualified by their standard deviations ($p < 0.05$); "ns" qualifies the variables that had not been selected after the model selection procedure. * $0.01 \leq p < 0.05$; ** $0.01 \leq p < 0.001$; *** $p \leq 0.001$.

4 | DISCUSSION

The overall aim of this study was to provide an effective framework to describe various crop sequences according to the environmental variability they generate, in order to go beyond the traditional monoculture–crop rotation opposition. We approximated the temporal variability by computing the diversity of crop height (a proxy of light availability for weeds), sowing dates (a proxy of disturbances timings) and herbicide spectrum (a proxy of disturbances types) that arise from various crop sequences, assuming that these factors were the main environmental drivers for weeds (Bohan et al., 2011; Perronne, Le Corre, Bretagnolle, & Gaba, 2015). Besides providing a robust comparative method, we describe crop sequences according to the mechanisms that may affect weed community assembly, that is variability in disturbances and in resources availability. Doing so, we highlight that the variability in disturbances and of resources availability differentially affect weed diversity and abundance (discussed below). These results provide an important scientific basis to justify the use of a particular crop sequence over another in order to reach a specific (weed) management goal (i.e. controlling weed abundance,

promoting weed diversity or both). Note that such scientific basis misses from crop sequence analyses, as recently discussed in a review (Dias et al., 2015). To fill this gap, future analysis could easily extend our framework by integrating others relevant crop functional traits (e.g. lateral spread) or farming practices (e.g. nitrogen fertilization) that may affect weeds or other taxa present in arable fields (e.g. soil microbial communities; Ingerslew & Kaplan, 2018). Studies with in situ measurement of crop height would also allow integration of fine scale variability in resources and consideration of intra-species variability.

In this study, we show that crop sequence diversity exerts a stronger influence on pluri-annual than on annual weed species pool, revealing the medium-to-long-term influence of crop sequence on weed community. These effects on pluri-annual weed richness and abundance mostly rely on the diversity of resources availability (i.e. *crop height*) and disturbance timings (i.e. *sowing date*). Contrary to our hypothesis, we found that weed richness increased with the diversity of disturbance timings. During a cropping season, weed community are dominated by species able to germinate soon after tillage (Crawley, 2004). Consequently,

TABLE 2 Model outputs for weed abundance (LM) in pluri-annual species pool and annual species pools at the beginning of a cropping season (T1 control), at the middle (T2 control) and in herbicide sprayed plots

	Pluri-annual	Annual T1 control	Annual T2 control	Annual T2 sprayed
Biogeographical gradients				
Longitude	-2.27 ± 0.75**	1.25 ± 0.34***	ns	0.75 ± 0.49
Latitude	ns	ns	-1.87 ± 0.49***	-3.16 ± 0.49***
Soil pH	-2.64 ± 0.68***	ns	ns	-0.83 ± 0.48
Year 2008	-	0.63 ± 0.47	1.21 ± 0.68	1.08 ± 0.65
Year 2009	-	1.38 ± 0.53**	1.75 ± 0.73*	2.05 ± 0.70**
Year 2010	-	1.37 ± 0.56*	-0.30 ± 0.89	-0.08 ± 0.88
Crop sequence diversity				
Resources availability	2.20 ± 0.99*	-0.69 ± 0.35*	0.17 ± 0.48	ns
Disturbance timings	-2.24 ± 1.03*	0.60 ± 0.35	ns	-0.29 ± 0.52
Disturbance types	0.03 ± 0.76	ns	-0.24 ± 0.50	1.15 ± 0.51*
Disturbance timings × disturbance types	-5.00 ± 2.38*	ns	ns	ns
Resources availability × disturbance types	6.64 ± 2.23**	ns	ns	ns
Management intensity				
Herbicide	-1.11 ± 0.70	-0.18 ± 0.34	0.27 ± 0.58	
Tillage	-1.03 ± 0.68	0.03 ± 0.34	-0.57 ± 0.25	-0.24 ± 0.49
Herbicide × tillage	-5.80 ± 1.26***	1.09 ± 0.56	-1.97 ± 0.98*	
Crop sequence diversity × management intensity				
Resources availability × tillage	2.61 ± 1.31*	ns	ns	ns
Resources availability × herbicide	ns	-2.31 ± 0.61***	-1.91 ± 0.97	ns
Disturbance timings × tillage	ns	ns	ns	1.11 ± 0.80
Disturbance types × herbicide	-2.67 ± 1.19*	ns	-1.94 ± 1.15	ns

Notes. Estimates are qualified by their standard deviations ($p < 0.05$); "ns" qualifies the variables that had not been selected after the model selection procedure. * $0.01 \leq p < 0.05$; ** $0.01 \leq p < 0.001$; *** $p \leq 0.001$.

increasing the diversity of disturbance timings across a crop sequence may promote the coexistence of weed species that differ in their germination periods (i.e. temporal niche differentiation). In contrast, pluri-annual weed abundance decreased with the diversity of disturbance timings, suggesting that unpredictable disturbance regimes can also increase the number of weed mortality events (Boyce, 1992). In addition, both pluri-annual weed richness and abundance increased with the diversity of crop height—a proxy of light availability for weeds in arable fields. There, light is the main limiting factor (Weiner et al., 2010) and weed species display different functional strategies in their use of available light (Storkey, 2005). Different weed responses to the temporal variability in light availability across crop sequences may thus promote weed coexistence in fields undergoing diversified crop sequence (Andrade et al., 2017; Chesson, 2000).

Contrary to our hypothesis, we found higher effects of crop sequence functional diversity on annual weed species pools at the middle than at the beginning of a cropping season. This could reflect that diverse crop sequences including spring crops before the studied winter-cereal cropping season will favour the expression of

spring germinating weeds that can only be recorded in the T2 survey (Borgy et al., 2016). We also found that contemporary herbicide sprayed decreases the influence of crop sequence diversity—particularly on annual weed abundance—confirming our hypothesis. Furthermore, the diversity of herbicides spectrum mainly affected annual weed richness in herbicide sprayed plots, suggesting that past herbicide treatments modulate the effects of contemporary herbicide treatment on weed communities (Doucet et al., 1999).

However, while we considered two major gradients of temporal variability, as well as management intensity and biogeographical gradients, a large part of the variance of weed richness and abundance remains unexplained (between 67% and 88%). This may reflect the important role that regional processes play on weed community assembly (Fried et al., 2008; Henckel, Borger, Meiss, Gaba, & Bretagnolle, 2015).

Finally, we assumed that temporal variability increases with the functional diversity of crop types inserted in the crop sequence. Yet, besides the diversity of crop characteristics, temporal variability also relies on the temporal arrangement of these characteristics across a crop sequence (i.e. *environmental predictability*, Menge & Sutherland,

1976). The effects of environmental predictability on weed communities has been explored theoretically by comparing equally diverse crop sequences that differ in the arrangement of the sequentially cultivated crop species (e.g. AABB vs. ABAB; Garrison, Miller, Roxburgh, & Shea, 2012; Garrison, Miller, Ryan, Roxburgh, & Shea, 2014; Mertens, Van Den Bosh, & Heesterbeek, 2002). However, because most of the real farming crop sequences are crop rotations (e.g. winter wheat–oil seed rape–winter barley), crop sequence diversity and environmental predictability importantly covary in real farming datasets. Future studies should therefore design crop sequences in order to disentangle crop sequence functional diversity—that is the diversity of crop characteristics over the course of a sequence—and environmental predictability—that is the order of crop characteristics over the same period—to understand how these two components of environmental variability affect weed diversity and abundance.

To conclude, this work highlights the important roles that crop sequences play in shaping weed community as well as its high potential to develop sustainable weed management strategies. Our results show that farmers can enhance weed diversity in their fields by sequentially sowing crop species that differ in their competitive ability and sowing dates. In addition, over the long-term they can achieve higher control of weed abundance by increasing the diversity of crop sowing dates across the crop sequence. Interestingly, while Doucet et al. (1999) advocated that the effects of crop sequence on weed abundance mainly rely on the variability in herbicides spectrum used across a crop sequence, we show that diversifying herbicides spectrum is less important than diversifying disturbance timings for controlling weed abundance in conventional farming systems. This would support the importance of diversifying disturbance timings to control weed abundance in low herbicides input cropping systems and in organic farming systems. A further step will be to investigate the influence of crop sequence functional diversity on both rare and competitive dominant weeds to better understand how crop sequence diversity affect weed diversity and to determine the crop sequences that would better balance food production and biodiversity conservation.

ACKNOWLEDGEMENTS

This study was partly funded by the French Ministry for Higher Education and Research through a doctoral grant (L.M.). F.G. and S.G. are funded by ANSES and INRA respectively. This study has been partly funded through the ANR (French National Research Agency) AGROBIOSE project (ANR-13-AGRO-0001). This paper was produced with the support of CESAB-FRB as part of the activities of the DISCO-WEED Working Group. We would like to thank the French Ministry of Agriculture who funded the national weed survey Biovigilance Flore and Dane Panetta for English revision.

AUTHORS' CONTRIBUTIONS

L.M., G.F. and S.G. planned and designed the research; L.M. analysed the data and wrote the first draft of the manuscript; G.F. and S.G.

contributed substantially to revisions. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.qf0k11c> (Mahaut, Gaba, & Fried, 2019).

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How to cite this article: Mahaut L, Gaba S, Fried G. A functional diversity approach of crop sequences reveals that weed diversity and abundance show different responses to environmental variability. *J Appl Ecol*. 2019;56:1400–1409. <https://doi.org/10.1111/1365-2664.13389>