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Landscape scale management affects weed richness but not weed abundance in winter wheat fields

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ABSTRACT

Farmland biodiversity provides ecological services that support food production, but the spatial scale(s) at which its management should be implemented is an acute question today. Effective management of weeds is a particularly hot issue as these plants can cause yield loss but support farmland biodiversity. In a general context of pesticide reduction, a clear understanding of how agricultural managements at different spatial scales interact with one another in shaping weed communities is required to develop sustainable weed management strategies. Here, we analyzed the contribution of potential drivers of weed species richness and weed abundance in 125 winter-wheat fields under a gradient of crop management intensity. We hypothesized that (i) local management practices in fields and (ii) the structure and composition of the landscape surrounding these fields would both explain the variations in weed richness and weed abundance observed within the study area. Linear mixed-effects models that included sequentially three sets of explanatory variables (farming system, local management practices, landscape structure and management) were applied and the relative performance of models was compared by AIC. Our analysis showed that weed species richness responded to factors acting at multiple spatial scales, with a predominant effect of landscape scale management, namely the proportion of organic farming within a 1 km radius. In contrast, weed abundance was difficult to predict and responded solely to few local management practices. As weed richness and abundance did not respond at the same spatial scales, we conclude that it may be possible to combine local and longer-term landscape management levers to deliver reduced weed infestation levels and enhanced arable biodiversity.

1. Introduction

In agricultural landscapes, the scale(s) at which biodiversity management should be implemented is an acute question (Tscharntke et al., 2005; Gabriel et al., 2010) as many farmland organisms contribute to ecosystem services impacting food production, e.g. pest control (Bohan et al., 2013; Crowder and Jabbour, 2014) or crop pollination (Deguines et al., 2014; Bretagnolle and Gaba, 2015). Among the taxa well-represented in agro-ecosystems, arable weeds are an interesting group (Petit et al., 2011) because they can potentially decrease crop production (Oerke, 2006; Mézière et al., 2014) while contributing to the maintenance of farmland biodiversity (Marshall et al., 2003; Requier et al., 2015).

The farming system type conducted in the focal field (i.e. conventional *vs.* organic) is known to affect weed richness (Gabriel et al., 2006; Ekroos et al., 2010). Few studies have however addressed the combined effect of factors occurring at multiple spatial scales and they have yielded conflicting results. In some situations, the landscape scale context appears to bear little or no effect on weed assembly compared to local management factors (Marshall, 2009; Armengot et al., 2011) while in other situations, a combined effect of local and landscape scale factors has been evidenced (Gabriel et al., 2006; José-Maria et al., 2010; Rundolf et al., 2010; Alignier et al., 2013; Henckel et al., 2015). Disentangling local and landscape scale effects on weeds may be hindered by a non-independence of factors measured at the two spatial scales (Boutin et al., 2008; Ekroos et al., 2010; Hawes et al., 2010), e.g.

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local organic management is more likely to occur in more complex landscapes (Norton et al., 2009) and the intensity of local management can be positively related to focal field size (Herzog et al., 2006). This latter point can raise problems for interpreting observed patterns, for example weed richness has been negatively related to field size (Gaba et al., 2010) but this relationship could either reflect a low amount of weed-rich uncultivated habitats or, alternatively, a more intensive local management of large fields (Aouadi et al., 2015). In addition, local and landscape scale factors can have interactive effects on weed richness, e.g. the effect of local management on weeds can change with the landscape setting (Concepcion et al., 2008) while landscape effects are sometimes only detected under specific local management (Gabriel et al., 2010). It is thus often difficult to assess the role of landscape scale factors on weed species richness, in comparison to local management practices.

In contrast to richness, the abundance or cover of arable weeds and their response to multiple scale factors is much less documented, despite the fact that such knowledge would be highly valuable for developing weed management strategies encompassing different spatial scales. Landscape factors are often considered to have little effect compared to local management (Ekroos et al., 2010), although a recent study established that the diversity of landscape elements that directly surrounded fields had a robust positive effect on in-field standing weed abundance (Bohan and Haughton, 2012).

Here we provide a thorough analysis of the relative importance of local crop management (including field size) and landscape scale factors, as well as of potential interactions between those factors, for predicting variations in weed richness. In addition, we expand our analysis to the prediction of weed abundance using the same multiple scale factors. Information on the weed flora, farming practices and landscape context was collected in 125 winter-wheat fields selected along a gradient of field size and in different farming systems types i.e. organic, agri-environment schemes (AES) and conventional farming. To disentangle the effects of field size, local farming practices and landscape context on weed diversity and abundance, we used a sequential multi-model selection framework. A first model investigated whether weed richness and abundance result from field size and farming system type (i.e. organic, AES and conventional), two factors that can be considered as integrative of multiple other variables. Then, keeping farming system and field size as explanatory variables, local factors, landscape factors, and finally their interaction were added sequentially. We thus tested whether models integrating detailed factors acting at the local or landscape scales would recreate and/or would outperform the first model in which field size and farming systems explain variations in weed richness and abundance in arable fields.

2. Material and methods

2.1. Study site and field selection

The data were collected in 2011 in the LTER Zone Atelier ‘Plaine & Val de Sèvre’ (c.a. 45000 ha; http://www.za.plainevalsevre.cnrs.fr/), an agricultural landscape dedicated mainly to winter cereal production and located in central-western France (46°11′N, 0°28′W). This study area is heterogeneous in terms of soil types, including shallow to deep red-limestone soils, clay and loamy soils. The most frequent crop rotations in the area were typically four-year long, based on winter wheat followed by winter oilseed rape, sunflower or maize. Almost 3% of the area was under organic farming and another 7000 ha were conducted under agri-environmental schemes (AES) aiming at reducing herbicide and N fertiliser inputs.

Field selection was conducted in a way that ensured a fair representation of the three farming systems and a good spatial spread of fields across the study area. When possible, three fields of different sizes (small, medium, large) were selected within a single farm. In total, we surveyed 86 fields in conventional farming, 25 fields under AES and 14 organic fields (Fig. 1). Field size did not significantly differ among farming systems with mean and standard error for field size of respectively 5.88 (4.25), 5.86 (3.42) and 6.34 (4.88) ha for conventional, AES and organic fields.

2.2. Weed sampling

Weed sampling was performed between 23rd March and the 16th April 2011. In each field, weed abundance was recorded within 10 plots of 2 m × 2 m that were located 10 m from each other along a line parallel to the field border and perpendicular to the crop rows. The first 4 m^2 plot was set 20 m from the field border. Weed species were identified at species level and the abundance of each

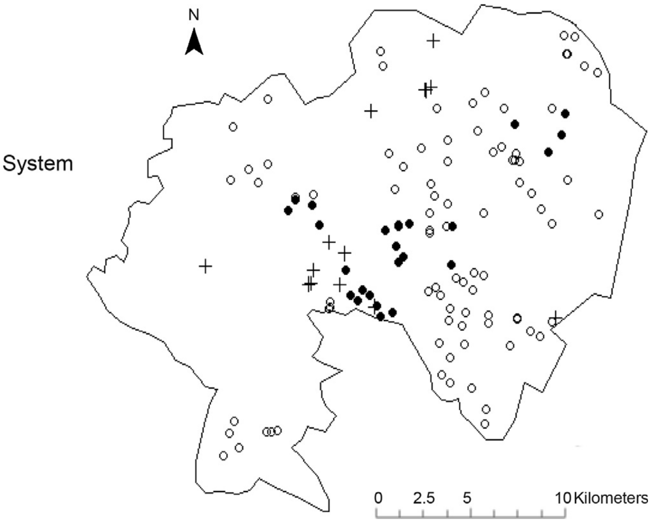

Fig. 1. Location of the 125 sampled wheat fields in the study area. Symbols represent the farming system type: cross = organic; dark circles = AES and empty circles = conventional.

species was recorded in six classes on a ten basis log scale (1 = 1 plant per plot; 2 = 2–9 plants per plot; 3 = 10–99 plants per plot, 4 = 100–999 plants per plot, 5 = 1000–9999 plants per plot). Data recorded within the 10 plots were pooled in order to estimate for each field (i) weed species richness i.e. the number of species found in all the quadrats of the field and (ii) weed abundance i.e. the sum of all individuals on the 10 quadrats sampled within the field with each species abundance per quadrat transformed from classes to number of plants by calculating the geometric mean of the limit values of each abundance class.

2.3. Local and landscape variables

Local management practices applied in each field – from the harvest of the previous crop to the weed sampling date – were recorded through interviews with farmers, with a focus on practices known to affect weed communities (see Gaba et al., 2014). Herbicide use was assessed by the Treatment Frequency Index TFI, i.e. the actual number of treatments and their dose as used by farmers out of full rates and full field application (Gravesen, 2003). The mechanical destruction of weeds was estimated by Mechanical operations i.e. summing up the number of operations of mechanical weeding per se and superficial and/or deep soil tillage operations. Crop Sowing day, crop Row spacing and nitrogen fertilization levels N input were also documented. This information yielded five variables (see Table 1 for average values and range).

To account for the landscape context of the sampled arable fields, we used the LTER Zone Atelier 'Plaine & Val de Sèvre' spatial land-use database which is updated yearly since 1995 and classifies land use into 42 types. The selected landscape metrics were the proportional cover of five land use types, namely %Forest, %Wheat, oilseed rape %OSR, %Grassland and %Alfalfa and two additional variables describing linear features i.e. the length of crop edges Edge length and the length of hedges Hedge length. From the updated database of farming systems of the LTER, we additionally extracted the proportional cover of area under organic farming % Organic, a factor previously evidenced to affect weed species richness in the study area (Henckel et al., 2015).

In order to assess the spatial extent that was the most relevant to explain weed richness and abundance, statistical models (see below) were run with variables computed respectively in circles centered on the barycenter of the sampled plots at radiuses of 200 m and 1 km (see Table 1 for landscape values at 1 km). Since Hedge length and %Grassland were highly correlated at both spatial extents (Pearson correlation, rho = 0.55, *p*-value < 0.0001), only the variable %Grassland was kept in further analyses, as the effect of grasslands on weeds has been previously evidenced in the study area (Henckel et al., 2015). The average value and range of the seven landscape variables are presented in Table 1.

2.4. Data analysis

We used a sequential model selection framework, i.e. all variables were not simultaneously included in a single model. Rather, each model sequentially tested the species responses to a specific set of variables, e.g. local or regional (see also Brodier et al., 2014; Henckel et al., 2015). Linear models (LM) and linear mixed models (LMM) were used to model weed richness and weed abundance (log-transformed), as both variables followed normal distributions. All explanatory variables were standardized with mean equal to 0 and standard deviation equal to 1 in order to allow for the comparison of the estimated coefficients. Model sequence included three steps; for each step, the best model was selected using the dredge option and models were compared by model averaging with the Akaïke Information Criterion weights (AICw) obtained for all possible sub-models (Barton 2013). At each step, we kept the selected response variables and used AIC based model averaging to fit LMs. Since conventional fields accounted for the majority of our sample, we replicated our model selection analyses to a subset of the data that only included the 86 conventional fields.

2.5. Field size and farming system

A first model examined whether the two synthetic variables, i.e. field size and farming system, could affect weed richness and abundance, in addition to two confounding factors, i.e. soil type (six categories) and preceding crop type (seven categories) (see Table 1, Model 1). Field size was either considered as a continuous factor (log transformed) or a factorial effect (three classes) with farmer identity as a random effect. Only two-way interactions were considered.

2.6. Integration of local management practices

The five local management practices were added to the model, i.e. N input, Mechanical operations, Herbicide, Row spacing and Sowing date, with all second-order interactions except with Sowing date (see Table 1, Model 2).

Table 1
Explanatory variables.

Variable	Description	Mean ± SD	Min – Max
Farming system type	3 classes: organic, AES, conventional		
Preceding crop	7 classes		
Soil type	6 types		
Field size	Focal field size (ha)	5.93 ± 4.14	0.34–18.72
Herbicide	TFI: Treatment Frequency Index	1.01 ± 0.62	0–2.83
Mechanical operations	Sum of mechanical weeding, superficial and deep tillage operations	2.08 ± 1.195	1–6
Sowing day	Julian day of the year of crop sowing (days)	297 ± 12	283–356
Row spacing	Distance between two seeding rows (cm)	14.64 ± 3.40	10–30
N input	Nitrogen fertilization applied (N units)	116.09 ± 48.64	0–240
%Organic	% area organic farming	3.98 ± 9.29	0–47.55
%Forest	% area of forest	4.05 ± 8.24	0–47.33
%Wheat	% area of winter wheat	35.53 ± 10.53	13.33–63.55
%Grassland	% area of grassland	13.01 ± 6.72	1.02–34.87
%Alfalfa	% area of alfalfa	7.13 ± 6.18	0.32–33.06
%OSR	% area of oil seed rape	7.45 ± 5.24	0–21.98
Edge length	Length of crop edges (km)	85.7 ± 14.5	45.25–120.05

2.7. Integration of landscape scale factors

In the following step, the seven landscape variables (at 200 m and 1 km) were tested sequentially for explaining weed abundance and richness. A significant effect of %Organic was detected which yielded higher estimates at the 1 km scale (results not shown). % Organic and the other landscape metrics estimated at the 1 km scale were thus added to the previous selected model (see Table 1, model 3). Possible two-way and triple interactions between local and landscape variables selected in the model were tested.

The same procedure was applied to the subset of 86 conventional fields (Model 4)

The full model and all possible subsets of the full model were analyzed using the multimodel inference package, MuMIn, in R (R Development Core Team, 2014; Barton, 2013). The overall best model and all competing models were identified and ranked using bias-corrected Akaike's Information Criterion (AICc). We considered all models with a ΔAICc < 2 to be supported by the data. Model-averaged coefficients were then calculated as weighted averages using model coefficients and AICw, where coefficients were set to zero when a variable was not included in a given model (Burnham and Anderson, 2002). We checked for spatial autocorrelation patterns by analyzing the model residuals using correlograms and Morans' I values against the distance between the fields, calculated with the R package "ncf" (Bjornstadt, 2012). No such autocorrelation was detected (results not shown).

3. Results

In total, 120 weed species were observed. Nine species – *Fallopia convolvulus* Löve, *Veronica hederifolia* L., *Polygonum aviculare* L., *Anagallis arvensis*,*Galium aparine*, *Mercurialis annua*, *Viola arvensis/tricolor*, *Chenopodium album* et *Papaver rhoeas* – known to be ubiquitous, were observed in ca. 50% of the sampled fields whereas 65% of species occurred in less than 10% of the sampled fields. Mean weed richness per field was 16.59 species and ranged from 2 to 37 species. Mean weed abundance per field was 1762 plants over the 10 four-m^2 plots and was below 5000 plants for all fields but five, where abundances were around or even higher than 10,000 plants (i.e., over 250 individual plants/m^2). Weed abundance and richness were significantly and positively correlated ($F_{1,123} = 28.75$, $p < 0.0001$). Overall, both species richness and total abundance (all species abundances cumulated) varied significantly with sampling date (respectively, LM, $F_{1,123} = 20.6$, $p < 0.0001$ and $F_{1,123} = 19.51$, $p < 0.0001$). Though a quadratic effect of sampling date yielded a significant effect, the slope was very close to 0. We thus linearly detrended both variables in order to correct richness and abundances for sampling date.

The first step of the sequential analysis (Model 1) revealed that neither the size nor the farming system of the focal field significantly explained weed richness and weed abundance, whether field size was represented as a continuous or as a factorial variable (ESM1). The second step of the procedure (Model 2) showed that some local management practices had a significant effect on weed richness and abundance (Table 2 for statistical effects and ESM2 for model AICw). Weed richness was affected positively by Row spacing ($p = 0.0097$) and a positive interaction between N input and Mechanical operations was detected, i.e. the negative effect of N input on weed richness decreased when Mechanical operations increased ($p = 0.00032$). N input affected negatively weed abundance ($p = 0.039$). All other variables (including TFI, but also field size and farming system type) were eliminated in the selection procedure. Row spacing effect on species richness was in fact due to only four fields (all organic) that had much higher values; when these four fields were removed, no significant correlation was found anymore. The integration of landscape scale factors in the third step (Model 3) revealed that % Organic affected weed richness markedly, whereas the effect of local management factors was limited to the positive interaction between N input and Mechanical operations (Table 3). %Organic neither interacted with N input nor with Mechanical operations, so there was no statistical support for an interaction between local and landscape scale factors. In this third step of the procedure, slope coefficients were of the same magnitude and sign, but *p*-values were overall slightly higher (Table 3). No landscape scale factor affected weed abundance but the negative impact of N input was still detected.

When the model selection was restricted to the 86 conventional fields (Model 4), the final selected model was not fundamentally different for weed richness (Table 4). Local management factors

Table 2
Model-averaged coefficients for Model 2 i.e. the effects of Field size, farming systems and individual farming practices and their interactions on (a) weed richness and (b) weed abundance.

	Estimate	Std Error	*Z* value	*P* value
(a) Weed species richness				
Intercept	17.8425	2.3118	7.678	<0.0001
Herbicide	−1.001	0.6815	1.455	0.145
Mechanical operations	0.3228	0.7336	0.436	0.663
N input	−0.6738	0.6106	1.092	0.275
Row spacing	1.5688	0.6006	2.586	< 0.01
Herbicide: N input	−0.771	0.6393	1.199	0.231
Mechanical: N input	1.9766	0.5449	3.594	< 0.001
N input: row spacing	−0.1997	0.4399	0.452	0.651
FS_AES	−0.6949	2.0932	0.330	0.742
FS_Conv	−1.1126	2.5259	0.439	0.661
Field size	−0.0615	0.3541	0.172	0.863
(b) Weed abundance				
Intercept	2.8771	0.1561	18.334	<0.0001
N input	−0.1071	0.0514	2.066	<0.05
Field size	−0.0568	0.0830	0.681	0.496
Mechanical operations	0.0259	0.0483	0.533	0.594
Row spacing	0.0289	0.0523	0.551	0.582
Mechanical: N input	0.0389	0.0598	0.649	0.516
N input: row spacing	−0.0349	0.0579	0.601	0.548
Mechanical: N input	−0.0068	0.0219	0.307	0.759
Herbicide	0.0016	0.0138	0.112	0.911

Table 3
Model-averaged coefficients for Model 3, i.e. the effects of Field size, individual local management practices and landscape scale variables on (a) weed richness and (b) weed abundance.

	Estimate	Std Error	*Z* value	*P* value
(a) Weed species richness				
Intercept	16.9772	1.2416	13.586	<0.0001
%Organic	2.7901	0.7365	3.752	0.000175
%Forest	−0.9881	0.5799	1.690	0.091
%Grassland	0.7701	0.6824	1.123	0.261
Mechanical operations	−1.0032	0.7202	1.379	0.168
N input	−0.8401	0.5815	1.430	0.153
Row spacing	0.4723	0.6469	0.730	0.465
Mechanical: N input	1.7022	0.4505	3.740	0.000184
Field size	−0.2398	0.6298	0.379	0.705
%Lucerne	−0.0456	0.2781	0.163	0.871
%OSR	0.0244	0.1783	0.136	0.892
(b) Weed abundance				
Intercept	2.8148	0.1144	24.459	< 0.0001
N input	−0.1093	0.0481	2.249	0.0245
Field size	−0.0249	0.0589	0.421	0.674
Edge length	0.0123	0.0324	0.378	0.706
%OSR	0.0027	0.0171	0.161	0.872
%Grassland	0.0023	0.0162	0.138	0.890
%Organic	0.0021	0.0161	0.130	0.897
%Forest	0.0016	0.0148	0.105	0.916

Table 4
Model-averaged coefficients for Model 4, i.e. the effects of field size, individual farming practices and landscape properties on weed richness in the subset of 86 conventional fields.

	Estimate	Std Error	*Z* value	*P* value
Intercept	14.3566	1.0288	13.784	<0.0001
%Organic	1.6605	0.6054	2.701	0.00692
Edge length	1.3092	0.6116	2.132	0.033
Mechanical operations	−0.0708	0.6824	0.114	0.909
N input	−0.7821	0.6252	1.232	0.218
Row spacing	0.8944	0.6294	1.399	0.162
Mechanical: row spacing	−1.6651	0.5851	2.801	0.005
N input: row spacing	−1.9508	0.6541	2.936	0.003
%Forest	−0.2763	0.5367	0.511	0.609
%OSR	−0.2328	0.4869	0.474	0.635
Field size	0.1059	0.4734	0.221	0.825

were present through three items that acted in interaction, namely N input, Mechanical operations and Row spacing. The two significant interactions Row spacing: Mechanical operations and Row spacing: N input eliminated the previously selected interaction N input: Mechanical operations. The positive effect of % Organic on weed richness was still significant, but a further term included Edge length and the magnitude of the effect of %Organic was less significant than when all farming systems were considered. No significant factor explained the variation in weed abundance in the conventional fields. i.e. the negative impact of N input was removed (ESM 3).

4. Discussion

In this paper, we explored variations in weed richness and weed abundance in a large subset of winter-wheat fields of varying size and under contrasted farming management. We found that weed richness was affected by some local management practices but mostly responded to landscape scale management, even in conventional fields. The prediction of weed abundance was limited and restricted to local management practices.

4.1. Predicting weed species richness

Our simplest model revealed that weed richness responded significantly neither to the size, nor to the type of farming system conducted in the focal field. This probably reflects the important diversity of management strategies that exists across our sampled fields within each of the farming system, as described in the study area by Lechenet et al. (2014). However, when focusing on detailed management practices, we found that some local farming practices affected weed richness, across farming systems and within the conventional farming system, which was dominant in our sample. Weed richness was positively affected by the width of the inter-row between winter-wheat sowings, a response that has been evidenced in winter-wheat in Spain (Guerrero et al., 2010) and which could reflect the increased occurrence of light-demanding summer annual species in wide inter-rows (Pinke et al., 2011). In our design however, this effect was mostly due to organic fields, which had higher inter-row spacing on average, and was less significant when only conventional fields were considered. The level of nitrogen fertilization was another local driver that affected weeds. A negative impact of N input was detected on weeds richness when the number of mechanical operation was low, i.e. reduced to one deep tillage or one superficial tillage operation). Reduced weed richness in the most nitrogen-rich arable fields has been evidenced in other large scale surveys (Gabriel et al., 2005; José-Maria et al., 2010; Lüscher et al., 2014) and is thought to reflect the filtering out of the least nitrophilous weed species, as evidenced by repeated surveys (Fried et al., 2009, 2012). Herbicide use did not affect weed richness but it is well established that detecting such signal in large-scale surveys is problematic (Gabriel et al., 2005; Marshall, 2009) and the negative impact of herbicide use on weed richness has rarely been established (but see Guerrero et al., 2010).

Increasing the spatial scale of models up to 1 km around the weed sampling point greatly improved our prediction of the observed variations in weed richness. This resulted from a strong positive effect of the proportional cover of organic farming at this scale which here exceeded the effect of local agricultural practices. More importantly, the cover of organic farming in the landscape was the main factor affecting weed species richness in the conventional fields. This result confirms the findings of Henckel et al. (2015) which were based on a weed survey of another set of conventional vs. organic wheat fields in the study area. These authors evidenced a linear increase of weed richness with the proportion of organic fields in the landscape both in organic and conventional fields, and showed that the integration of this landscape scale management factor in predictive models halved the effect of local organic management. This is an important result as the impact of landscape scale management on in-field weed richness has so far only been established for organic fields (Gabriel et al., 2010). The interpretation of Henckel et al. (2015) was that the occurrence of organic fields within a landscape dominated by conventional fields sustains a metacommunity dynamic with spatio-temporal flows of weed propagules, mostly from organic to conventional fields (source-sink dynamics, Pulliam, 1988). The idea that weed spatial dispersal may play a role in the variation of weed richness in conventional fields is reinforced here by the fact that crop edge density around conventional fields has a positive effect on in-field weed richness, as was established in previous studies (Gabriel et al., 2005; Concepcion et al., 2008; Guerrero et al., 2010). Landscape scale management has indeed been shown to increase weed richness in the field margins of both organic and conventional fields (Rundolf et al., 2010). Here, conventional fields that sit in a landscape context that combines a high cover of organic fields and a high density of field edges are thus harboring enhanced weed richness. The underlying mechanisms act at two spatial scales and are thus strongly shaped by farming activities at different organizational levels – field and its margin – farm and landscape (Petit et al., 2013). Within a 1 km radius, the propagule pool is dependent on the ratio of organic management at that scale and seed spatial dispersal can be partially enhanced through a network of arable field margins; at a smaller spatial scale, mass effect takes place, thus enabling the entry of weed species from the margin to the core of fields (Poggio et al., 2010).

4.2. Predicting weed abundance

We detected no effect of the farming system on weed abundance. The integration of a set of management practices known to potentially affect weed abundance and of landscape scale factors revealed little response to these factors, and always limited to local scale factors. A negative impact of N input on weed abundance was detected across farming systems, but this effect was not detected when our analysis was restricted to fields conducted with a conventional farming system. In addition, one would have rather expected a positive impact of N input on weed abundance. The level of herbicide use did not come out as a significant factor affecting weed abundance. Because high nitrogen availability is likely to promote weed growth and abundance of weeds that are more nitrophilous than the wheat crop (Moreau et al., 2013), one would have expected a positive response to N input across systems. Because N input and herbicide use were positively correlated in our sample, we cannot completely rule out the possibility that the negative relationship between weed abundance and N input masks a negative effect of herbicide use. However, the lack of response to herbicide use could also result from the fact that most farmers adapt their herbicide regime to the density of weeds they observe in their field so that contrasted levels of herbicide use may result in a similar end-result in terms of weed abundance. It is also important to bear in mind that TFI is a proxy for herbicide use and does not inform on the efficacy or the toxicity of the herbicide application in the field. Finally, other local variables, not analyzed here, may have produced different outcomes; for instance, preceding crops other than the next precedent may better account for the seed bank, and thus better predict weed abundance (see e.g., Bohan et al., 2011).

4.3. Implications for management

A key challenge in managing annual weed communities is to maintain effective control of problematic weeds whilst enhancing the occurrence of diverse communities that can support ecosystem services (Bretagnolle and Gaba 2015). A clear understanding of how agricultural activities at different spatio-temporal scales interact with one another in shaping weed communities is required to develop integrated weed management strategies. Our results highlight the complexity of factors, which alone or in interaction, drive weed richness and abundance in winter-wheat fields. They also indicate that the nature and the scale at which the drivers act are not the same for weed abundance and weed richness, the latter responding at larger spatio-temporal scales. This suggests that it might be possible to combine landscape and local management levers to deliver reduced weed infestation levels and enhanced weed diversity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.02.031.

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