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Patch dynamics and temporal dispersal partly shape annual plant communities in ephemeral habitat patches

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Most organisms in ephemeral habitat patches have resting stages which form a local species pool in response to temporal variations in the patch's availability and suitability. Temporal dispersal from the local species pool may, therefore, be an important process shaping the community assembly, particularly soon after patch creation, and possibly interacting with environmental filtering. As the temporal variation of the environmental conditions has a major effect on the composition of the local species pool, we investigated how well contemporary conditions (both patch availability and patch suitability) and temporal dispersal (approximated by environmental temporal variation and temporal distance) explain the changes in community composition in a given locality through successive ephemeral habitat cycles. We used arable weeds in annual crops as models. We calculated temporal weed community dissimilarity indices between weed communities surveyed in cropping seasons at intervals of two to eight years within a given field. The weeds were surveyed twice each cropping season to account for any changes in the relative contributions of temporal dispersal and contemporary conditions during the season. Patch availability explained most of the temporal weed dissimilarity, suggesting that patch dynamics have the greatest effect on weed community assembly. Temporal distance and temporal variation of the environmental conditions had more effect at the start of the cropping season than later, while patch suitability had more effect in the middle of the season. These results suggest that temporal dispersal drives the weed community assembly when ephemeral habitat patches are created. These assemblies are further shaped by environmental filtering. This is consistent with a temporal source–sink dynamic mechanism where the seed bank acts as the main weed source. However, a large part of temporal weed dissimilarity remains unexplained, suggesting that other ecological processes such as spatial dispersal and founder effect may also shape the weed community.

Introduction

In recent years, community ecology has improved the understanding of species assemblies by recognizing the combined role of local and regional processes in spatially and temporally heterogeneous environments. Much emphasis has been put in disentangling the role of local and regional factors within a metacommunity framework (Leibold et al. 2004). While local factors refer to the characteristics of the local habitat, such as

abiotic conditions or biotic interactions, regional factors generally refer to the spatial characteristics of the region that may affect local communities such as connectedness, abundance of source habitats, or characteristics of the regional species pool. However, temporal characteristics may also affect local communities, since most landscapes are dynamic, resulting in changes in habitat availability and suitability with time ("harlequin landscape", Horn and MacArthur 1972, Leibold and Loeuille 2015).

High temporal variations in the habitat patch's availability and suitability are notably found in temporary ponds, which are ephemeral habitat patches' (Jeffries 2008, Ferreira et al. 2015), or in deserts (Venable 2007) and agricultural landscapes (Reigada et al. 2015), both sheltering ephemeral habitats patches where environmental conditions allowing species to establish and successfully reproduce have restricted limited period of existence. Ephemeral habitat patches are characterized by a high proportion of species with resting stages, such as resting eggs for some planktonic crustaceans (Jeffries 2011) or dormant seeds for annual plants (Venable 2007), which form a local species pool (e.g. seed bank of dormant seeds) and avoid unsuitable environmental conditions through delayed emergence (temporal dispersal). Since community assemblies in ephemeral habitats depend on patch colonization (Reigada et al. 2015) and because the role of temporal dispersal via a local reservoir of propagules may be more important than spatial dispersal, as in ruderal plant population dynamics (Falahati-Anbaran et al. 2014), temporal dispersal is expected to be a main driver of community assembly in ephemeral habitats. Moreover, the limited period for which individual patches are available for species establishment and development, as well as the timing of the appearance of new suitable patches, are major factors shaping communities in ephemeral habitat. Indeed, the synchrony between patch availability and life cycle (both timing of dispersal and life cycle duration) of the species present in the local species pool are important factors shaping communities (Kim and DeWreede 1996). Additionally, the habitat patch suitability, both in terms of abiotic environmental factors and biotic interactions, such as competition, may further shape community assembly in these habitats either by favoring or being less suitable for species. The effect of patch suitability on community assemblies may increase with the duration for which the patch is available (Ferreira et al. 2015). As a result, the temporal variation of patch availability and patch suitability directly affects the composition of the propagule reservoir (Jeffries 2008, 2011), which, in turn, may affect the contemporary community assembly. The community assembly in ephemeral habitats may, therefore, result from the interaction between contemporary factors (patch availability and patch suitability) and temporal dispersal (temporal variation of environmental conditions and temporal distance).

In this study, we assessed the respective contribution of contemporary factors and temporal dispersal in shaping the community assembly in ephemeral habitat patches, using arable weeds as models. Weeds are an ideal system since they are predominantly annual species producing dormant seeds in a seed bank (Lewis 1973). A weed community is here defined as all the weed species present during a cropping season in an arable field while local weed species pool refers to the arable field seed bank. We consider that a cropping season (i.e. the growing period of the crop) is an ephemeral habitat patch for weeds, which can only develop between crop sowing date (i.e. the patch creation date) and crop harvesting date (i.e. the patch destruction date). Indeed, crop sowing and harvest represent major disturbances of the habitat; crop sowing being associated with soil tillage and harvest by biomass removal. In other words, we define ephemeral habitat as the period when crops are planted which delineates the timing during which weeds can grow and produce seeds in an arable field.

Decay of similarity (Nekola and White 1999) in community composition with geographic and environmental distances has been widely used to disentangle the relative contribution of local factors and spatial dispersal. We therefore analyzed the dissimilarity of weed community composition between weed communities present in the same arable field, but at different times (i.e. different cropping seasons) along the crop sequence, the 'temporal weed community dissimilarity' (Fig. 1A), and tested the following hypotheses:

- Patch availability, both the timing of patch creation and duration for which weeds can develop, is expected to be the main driver of the weed community assembly. Crop sowing date, a proxy for patch creation and duration (Gunton et al. 2011), has often been shown to be the most important driver of weed community assemblies in arable fields (Fried et al. 2008, Perronne et al. 2015, Seifert et al. 2015).

- The importance of patch suitability in shaping the weed community may increase during the cropping season, reducing the dominant effect of patch availability. During the cropping season, patch suitability for weed species depends on the use of tillage and herbicides (Hyvönen and Salonen 2002), and resource depletion induced by the growth of crop plants (Weiner et al. 2010). These interact with the climatic conditions, precipitation and temperature, which affect both herbicide efficiency (Jursík et al. 2013) and plant growth which, in turn affects resource competition (Ding et al. 2016).

- Temporal weed community dissimilarity increases with the temporal distance (i.e. number of cropping seasons) and the temporal variation of environmental conditions throughout the interval between the two surveys. The seed bank composition depends on the seed production of the previous season (Ryan et al. 2010) and its diversity is expected to increase with the temporal variation of the environmental conditions across cropping seasons (Anderson et al. 2007).

Material and methods

Data set

Data was taken from the long term French monitoring program Biovigilance Flore in which 1440 fields were
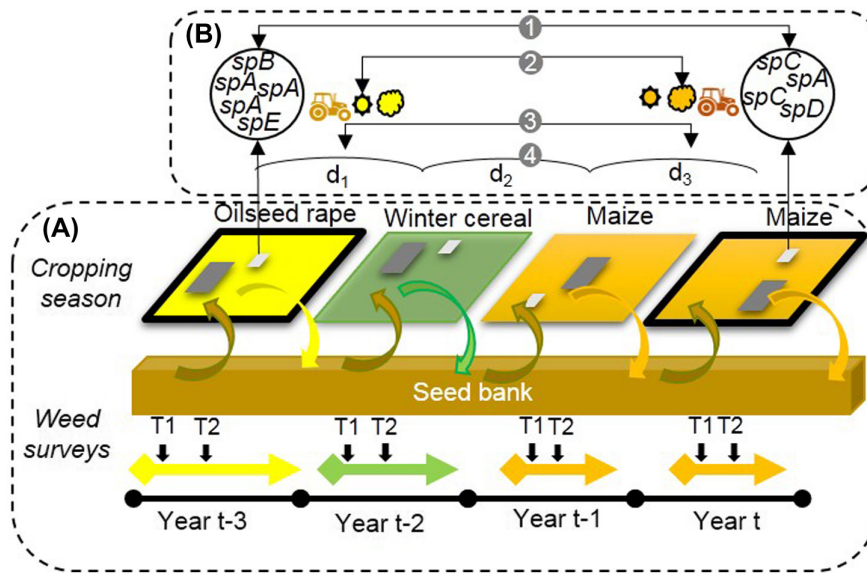
Figure 1. (A) Schematic representation of a four-year crop sequence in a field. The crop sequence consists in four annual crops, oilseed rape, winter cereals and two maize. These crops are characterized by environmental and agricultural conditions (the patch suitability) and by cropping season start date and duration (colored arrows, the patch availability) which starts with sowing and ends with the harvest. During the cropping season, two weed surveys were performed, one at the beginning of cropping season (T1) and one at the middle of cropping season (T2) in two plots: a sprayed plot in which herbicides are sprayed and a control plot in which no herbicides are sprayed. During the cropping season, weeds from the seed bank are reestablished, and successful weeds produce seeds that refill the seed bank. (B) Components of the analysis. For each pair of cropping season (here surrounded in bold), the dissimilarity in weed composition (1), the difference in environmental (mean annual temperature and total annual precipitation) and agricultural conditions (crop sowing date, tillage system, herbicide spectrum and crop height) (2) are calculated by calculating the distances for each parameter between the two cropping seasons compared. The temporal distance (3) is assessed as the number of cropping seasons separating the two cropping seasons compared. Lastly, temporal variation of environmental and agricultural conditions (4) are calculated as the mean of each environmental and agricultural distance calculating between each successive cropping season separating the two cropping seasons compared (i.e $(d_1 + d_2 + d_3)/3$; d_1, d_2 and d_3 being calculated for each environmental and agricultural factor; more details in Supplementary material Appendix 1).

monitored across France (761 km north–south, 696 km east–west) between 2002 and 2010. The fields were selected to represent the diversity of agricultural practices and environmental conditions in France (Fried et al. 2008) covering twenty major crop species (Gunton et al. 2011). Weed species were surveyed twice a year in 2000-m² plots subject to contemporary land management practices ('sprayed plots') and in ~140-m² plots with the same practices but excluding herbicides ('control plots'). Survey dates were adapted to the crop species: the first survey (T1) was carried out one month after sowing the crop, before post-emergence herbicide treatment, and the second survey (T2) was carried out in March–April for winter-sown crops and in July–August for spring and summer-sown crops after the last herbicide treatment. Species abundances were recorded using a semi-quantitative scale ('+' found once in the plot; '1' less than 1 individual m⁻²; '2' 1–2 individuals m⁻²; '3' 3–20 individuals m⁻²; '4' 21–50 individuals m⁻²; '5' more than 50 individuals m⁻²). For each cropping season, crop species as well as management practices such as herbicide treatments and tillage operations were recorded. A total of 348 weed species were recorded.

Data selection

Analyses were performed separately for the first and the second surveys of control plots ('T1 control' and 'T2 control'), and for the second survey only in sprayed plots ('T2 sprayed') to ensure that the plots had been sprayed with herbicide. For each field, pairs of cropping seasons along the crop sequence were selected to take the temporal variation into account. Pairs were separated by at least one cropping season. The mean number of cropping seasons per field was 5.22 (± 1.39; n = 472), 5.01 (± 1.44; n = 457) and 4.97 (± 1.41; n = 424) for T1 control, T2 control and T2 sprayed plots, respectively. A total of 1834, 1661 and 1400 pairs of cropping seasons were analyzed in the T1 control, T2 control and T2 sprayed sub-datasets respectively.

Temporal weed community compositional dissimilarity

To disentangle the roles of contemporary factors and temporal dispersal on the weed community assemblies, we calculated the temporal distance decay (Nekola and White 1999) in weed community composition by calculating temporal

dissimilarity indices between weed communities observed in each of the cropping seasons of the pair selected along the crop sequence in a field (Fig. 1B). We used the Jaccard dissimilarity index (based on presence–absence data), and Bray–Curtis dissimilarity (based on species abundance) to calculate the weed temporal dissimilarity indices using 'designdist' from the vegan R library (Oksanen et al. 2015).

Patch availability

The crop sowing date controls both the timing of patch creation and the length of the crop life cycle: crops sown in autumn generally have a long life cycle of about ten months, while crops sown in spring have shorter life cycle of about five months in France (Gunton et al. 2011). We therefore used crop sowing date as a proxy for both the timing of patch creation and patch duration to describe 'patch availability'. The distances between crop sowing dates for each pair of cropping seasons in a crop sequence represented the differences in 'patch availability' between pairs of cropping seasons (Fig. 1B; details in Supplementary material Appendix 1). To allow for the circularity of the dates, the day of the year was transformed into radians so that each day of the year could be represented as the cosine and sine of the day where the 1st of January was $\cos = 0$ and $\sin = 1$. A Euclidian distance matrix was then calculated between each cropping season of a pair using both the cosine and sine of the sowing day of year (Table 1).

Patch suitability

As the response variables are temporal dissimilarity indices between weed communities at two dates, patch suitability was characterized by the temporal difference in the main farming practices used for weed control (herbicide application and tillage system), climate conditions (precipitation and temperature), and the competitive ability of the crop species. The difference in the main target species of herbicide applications (i.e. herbicide spectra) between the two cropping seasons of a pair was analyzed using the Herbicides resistance action committee (HRAC) classification (<http://hracglobal.com/tools/classification-lookup> visited on August 2015) which groups active ingredients according to their site(s) of action. In total 108 different active ingredients corresponding to 20 HRAC groups were recorded in the Biovigilance Flore dataset (Supplementary material Appendix 2 Table A2–A1). We calculated a HRAC group distance matrix based on the Jaccard index to account for herbicide spectrum dissimilarity between the two cropping seasons of each pair. Tillage intensity, was classified as 1) 'conventional' for moldboard plowing where seeds from the previous season were buried (inversion tillage) and 2) 'minimum' for no-till or reduced tillage where previously produced seeds were not buried. Differences in tillage system between the cropping seasons of a pair were represented by one of the four combinations: conventional–conventional ('conv–conv'), conventional–minimum ('conv–min'), minimum–conventional ('min–conv') and minimum–minimum

('min–min') with the first term corresponding to the earlier cropping season of the pair and the second term to the later cropping season of the pair. Differences in climatic conditions were calculated using Euclidean distances between the mean annual temperature and total annual precipitation for each French administrative region (n = 21), for each of the nine years of Biovigilance Flore monitoring, using data from the INRA AgroClim application (<https://intranet.inra.fr/climatik> visited on August 2015). Finally, crop height was used to represent the crop species competitive ability. Indeed, plant height can be considered as a proxy for plant species competitive ability for light (Violle et al. 2009). We used average values of crop height from Gunton et al. (2011) and calculated the Euclidean distance between the heights of the crops grown in each cropping season of the pair (Fig. 1B). An example of all the metrics calculation is given in Supplementary material Appendix 1.

Temporal distance and temporal variation

We calculated the number of cropping seasons separating the two cropping seasons in a pair to take the temporal distance into account. Then, temporal variation of patch availability and patch suitability were calculated to take into account the temporal variation of the environmental conditions throughout the interval between the two cropping seasons in a pair. Temporal variation of patch availability was calculated as the mean distance between sowing dates for each pair of successive cropping seasons in the crop sequence delimited by the two cropping seasons (Fig. 1B). Temporal variation in patch suitability was calculated as the mean distance between the crop heights, herbicide spectra precipitations and temperatures, for each pair of successive cropping seasons in the crop sequence delimited by the two cropping seasons, and as the number of changes in tillage practices (conventional tillage or minimum tillage) between the two cropping seasons, normalized by the temporal distance.

Analysis

We investigated the effect of contemporary factors (patch habitat availability and patch suitability) and temporal dispersal (temporal distance and temporal variation) on temporal weed dissimilarity indices (Jaccard and Bray–Curtis indices) using linear mixed models (lmer, R library 'lmerTest', Kuznetsovat et al. 2015) to take account of the non-independence between observations with the field as a random effect (several pairs of cropping seasons per field). Models were run separately for T1 control, T2 control and T2 sprayed plots.

We used an Akaike information criterion (AIC) multi-model selection framework (Garamszegi 2011) to evaluate the extent to which the data supported three competing models of increasingly complexity. The model selection procedure was based on minimizing the AIC, starting with all two-way interactions and main effects. All retained covariates of the lower-level models were included in the more complex models. The first model included the effects of

Table 1. Mean and standard deviation of the covariates used in the three competing models in control plots at the beginning and in the middle of the cropping season (T1 control and T2 control plots) and in the middle of cropping season in herbicide sprayed plots (T2 sprayed plots).

Factors	Group	Covariates	Description of the value	T1 control	T2 control	T2 sprayed	Reference
Contemporary factors	Patch availability	Sowing date	Euclidean distance between two cropping seasons based on the sowing day (sin and cos)	0.84 (± 0.81)	0.82 (± 0.81)	0.82 (±− 0.81)	Biovigilance
	Patch suitability	Herbicide spectrum	HRAC Jaccard index between two cropping seasons	−	−	0.75 (± 0.31)	Heap 2006
		Height	Euclidean distance between two cropping seasons based on mean crop height (m)	0.36 (± 0.46)	0.35 (± 0.46)	0.35 (± 0.45)	Gunton et al. 2011
		Temperature	Euclidean distance between two cropping seasons based on mean annual temperature per administrative regions (°C)	0.67 (± 0.52)	0.67 (± 0.50)	0.67 (± 0.50)	AgroClim
		Precipitation	Euclidean distance between two cropping seasons based on total annual precipitation per administrative region (mm)	127.80 (± 135.81)	129.30 (± 140.68)	131.70 (± 141.36)	AgroClim
		Tillage intensity	Four combinations depending on the tillage system of each cropping season of a cropping season pair	conv–conv: 796 min–min: 510 conv–min: 313 min–conv: 215	conv–conv: 712 min–min: 473 conv–min: 277 min–conv: 199	conv–conv: 579 min–min: 425 conv–min: 222 min–conv: 174	Biovigilance
Temporal factors	Temporal distance	Temporal distance	No. of years separating the two cropping seasons of a pair	3.00 (± 1.12)	3.00 (± 1.07)	2.91 (± 1.04)	Biovigilance
	Temporal variation	Sowing date	Mean euclidean distance of the sowing day between successive cropping seasons	1.04 (± 0.65)	1.02 (± 0.65)	1.03 (± 0.65)	Biovigilance
		Herbicide treatment	Mean HRAC Jaccard index between successive cropping seasons	0.01 (± 0.07)	0.01 (± 0.07)	0.02 (± 0.07)	Heap 2006
		Height	Mean euclidean distance of the crop height (m) between successive cropping season	0.47 (± 0.36)	0.45 (± 0.36)	0.45 (± 0.36)	Gunton et al. 2011
		Temperature	Mean euclidean distance of the mean annual temperature per administrative region (°c) between successive cropping season	0.59 (± 0.36)	0.60 (± 0.36)	0.61 (± 0.36)	AgroClim
		Precipitation	Mean euclidean distance of the total annual precipitation per administrative region (mm) between successive cropping season	156.16 (± 117)	156.9 (± 119)	157.10 (± 115)	AgroClim
		Tillage system	Number of tillage system changes between successive cropping seasons	0.19 (± 0.29)	0.19 (± 0.29)	0.18 (± 0.29)	Biovigilance

patch availability (distance between crop sowing dates) and patch suitability (i.e. distances between herbicide spectra, crop heights, mean annual temperatures, total annual precipitations and tillage practices). Herbicide distances were only considered for T2 sprayed plots as there was no herbicide application in T1 and T2 control plots. In the second model, temporal distance was added to the variables selected for the first model in order to test whether weed community temporal dissimilarity increased with the temporal distance between the two cropping seasons. The third model was used to investigate the relative importance of the roles of temporal variation (variation of crop sowing date, herbicide spectrum, crop height, tillage system and climatic conditions) and patch availability, patch suitability and temporal distance. We standardized all variables before analysis. Before each selection procedure, the parameters were tested for multicollinearity as this can significantly increase the variance of the parameter estimates (O'Brien 2007). We calculated the variance inflation factor (VIF) using the 'vif.mer' function (<https://raw.githubusercontent.com/aufrank/R-hacks/master/mer-utils.R>) to detect severe multicollinearity (Belsley et al. 1980). For a value of VIF less than 10, the collinearity is negligible. We did not find severe collinearity for any of the models (VIF < 8.66 in all cases). After the selection procedure, we calculated marginal and conditional R^2s to estimate the fraction of the variance explained by the fixed effect only and by the fixed plus random effects (Nakagawa and Schielzeth 2013). We used the sum of the square of each explicative variable given by the ANOVA (type III) function from the car R library (Fox and Weisberg 2011) to evaluate the contribution of each covariate selected (Ginot et al. 2006).

As a given cropping season may have been used in several pairs of cropping season, we further quantified the bias induced by such a non-independence by computing the standardized effect size of the relative contribution of each covariate selected from the model selection procedure (Gurevitch et al. 1992, Gotelli and MacCabe 2002). The standardized effect size measures the number of standard deviations that the observed metric is above or below the mean metric, the mean and standard deviation being computed from simulated data (Gotelli and MacCabe 2002). To do so, we used a bootstrap resampling technique: we generated 2000 sub-datasets by randomly selected 500 cropping season pairwises with replacement among the 1834, 1661 and 1400 pair-wises respectively for T1 control, T2 control and T2 sprayed. We ran all previously selected models on every random sub-datasets and computed the standardized effect size of each covariate relative contribution (details in Supplementary material Appendix 3). We tested the null hypothesis that the average standardized effect size is zero by calculating the SES 95% non-parametric confidence interval (DiCiccio and Efron 1996, Davison and Kuonen 2002): if the latter did not include zero, therefore we observed a significant bias in the relative contribution of the focus covariate. No significant bias were detected by the standardized effect size analysis

(Supplementary material Appendix 3 Fig. A3–1 to A3–6). All analyses were conducted in R ver. 3.2.3 (<www.r-project.org>).

Data deposition

Results

Mean weed richness for control plots at the beginning of cropping season (T1 control), at the middle of the cropping season (T2 control) and for sprayed plots at the middle of the cropping season (T2 sprayed) were 7.31 ($\pm$ 4.97), 8.87 ($\pm$ 5.11) and 5.63 ($\pm$ 4.04), respectively. Mean Jaccard indices were 0.797 ($\pm$ 0.16), 0.780 ($\pm$ 0.15) and 0.839 ($\pm$ 0.16), respectively and mean Bray–Curtis indices were 0.834 ($\pm$ 0.15), 0.819 ($\pm$ 0.14) and 0.877 ($\pm$ 0.14) respectively. Both temporal weed community dissimilarity indices were significantly higher for T2 sprayed plots then for T1 control and minimum in T2 control plots (post hoc test on Kruskal test; $\chi^2 = 153.09$, df = 2, p < 0.0001 for Jaccard index and $\chi^2 = 188.16$, df = 2, p < 0.0001 for Bray–Curtis index).

Major role of crop sowing dates in shaping the weed community soon after patch creation

At the beginning of cropping season (T1 control plots), the third model had the lowest AIC score (Supplementary material Appendix 2 Table A2–2), indicating that this model was the most parsimonious model for both presence–absence (Jaccard) and abundance (Bray–Curtis) indices. The fixed effects from this model explained 14.0% of the Jaccard index variance and 15.5% of Bray–Curtis index variance (see marginal R^2 in Fig. 2). When field identity (random factor) was taken into account, the explicative power increased markedly; for example, for the Jaccard index, field identity explained about 22% of the explained variance (see the difference between marginal R^2 and conditional R^2 in Fig. 2).

Firstly, the distance in crop sowing dates, the proxy of patch availability, was by far the main factor affecting both the Jaccard and the Bray–Curtis dissimilarity indices (Fig. 2). The higher the distance in crop sowing dates, the higher the dissimilarity indices (Fig. 3A–B). Secondly, the difference in tillage intensity had a marked effect on both dissimilarity indices (about 10% of the explained variance, Fig. 2). Conv–min, min–conv and min–min systems had greater values of temporal weed community dissimilarity than conv–conv tillage systems (Table 2, 3). No other covariates used to characterize the patch suitability were retained as significant in the model selection procedure for the Jaccard index (Table 2) while the distance in temperature slightly affected the Bray–Curtis index which decreased as the distance mean annual temperature increased (Table 3). For the Jaccard index, there
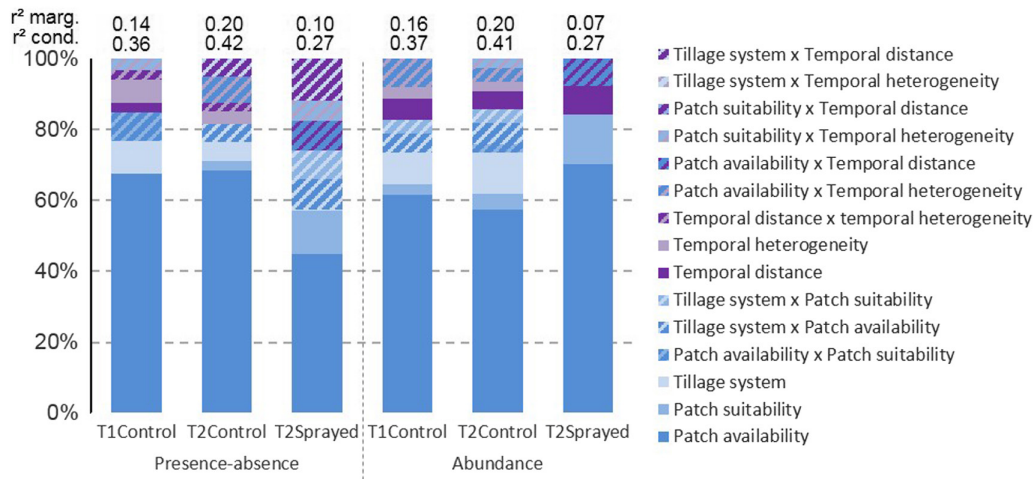
Figure 2. Relative contribution of contemporary factors (patch availability and patch suitability), temporal distance and temporal variation to the temporal dissimilarity of the weed community assemblies based on presence–absence data (Jaccard index) and species relative abundance data (Bray–Curtis index) for weed surveys conducted at the beginning of the cropping season (T1) and at the middle of the cropping season (T2) in control and sprayed plots. The relative contribution of each selected covariate is the percentage of the total sums of square of the model for each selected covariate. This is represented by the different colors in each bar, with blue for contemporary factors and pink for temporal factors. The total variance explained by fixed effects (marginal R²) and the variance explained by the complete model (conditional R²), with both fixed and random effects, are presented at the top of the bar. As an example, at the beginning of cropping season in control plot (T1 control) the difference in patch availability (in dark blue) accounted for nearly 68% of the total percentage of variance explained by the fixed effect of the model (marginal R² = 0.14 for the Jaccard index (presence–absence).

was a significant positive interaction between crop sowing date and annual precipitation and between crop sowing date and crop height (Table 2). For the Bray–Curtis index there was significant interaction between tillage and sowing date and between tillage and temperature with conv–min, min–conv and min–min tillage reducing the effect of the crop sowing date while increasing the effect of distance in temperature (Table 3). The temporal distance had a significant effect on the Jaccard and Bray–Curtis indices (about 3% of the explained variance for the Jaccard index and about 5% for the Bray–Curtis index, Fig. 2). Both indices increased with temporal distance (Fig. 3C–D). Temporal variation of environmental conditions also affected both dissimilarity indices (Fig. 2). This was largely due to a negative interaction between the temporal variation of crop sowing date and the temporal variation of crop height (Table 2, 3). Nevertheless, the temporal factors explained a much lower fraction of the explained variance than the contemporary factors: 12.09% versus 84.73% for the Jaccard index and slightly less at 9.40% versus 82.65% for the Bray–Curtis index (Fig. 2). Finally, interactions between contemporary factors and temporal variation explained about 3% of the explained variability of the Jaccard index and about 8% of the Bray–Curtis index (Table 2, 3).

Changing relative contribution of patch suitability and temporal factors at the middle of cropping season

For the middle of the cropping season in the control plots (T2 control plots), the third model also had lowest AIC score (Table A2), with the temporal weed community dissimilarity

at the middle of cropping season explained by contemporary factors, temporal distance and temporal variation. The covariates selected for the third model explained more of the temporal weed community dissimilarity than for T1 control plots with 19.8% of Jaccard index variance and 19.6% of Bray–Curtis index variance explained for T2 control plots (see R² marginal in Fig. 2). Distance in crop sowing date remained the principal factor shaping weed community assembly (Fig. 2). Distance in crop sowing date had a stronger effect on the Jaccard index distance than for T1 control plots (0.072 ± 0.005, p < 0.001, Fig. 3A, Supplementary material Appendix 2 Table A2–3) while the effect was weaker for the Bray–Curtis index (0.068 ± 0.005, p < 0.001, Supplementary material Appendix 2 Table A2–4, Fig. 3B). Conversely, the effect of patch suitability, on the Bray–Curtis index was much greater for T2 control plots (Fig. 2). Furthermore, total annual precipitation had a positive effect on both indices (0.011 ± 0.004, p = 0.004 for Jaccard and 0.008 ± 0.004, p = 0.031 for Bray–Curtis, Supplementary material Appendix 1 Table A3–A4). A positive interaction between crop height and crop sowing date also affected the Bray–Curtis index. Taken together, the relative contributions of contemporary factors (81.54% for the Jaccard index and 85.59 % for the Bray–Curtis index) were similar to those for T1 control plots. Also, the relative contribution of temporal factors to the explained variance of the Jaccard index was much lower (about 6%, Fig. 2) than for the T1 control plots, while for the Bray–Curtis index the contribution was similar (about 8%, Fig. 2). The contribution of temporal distance was no longer significant for the Jaccard index (Fig. 2). The contribution of temporal variation for the Jaccard and
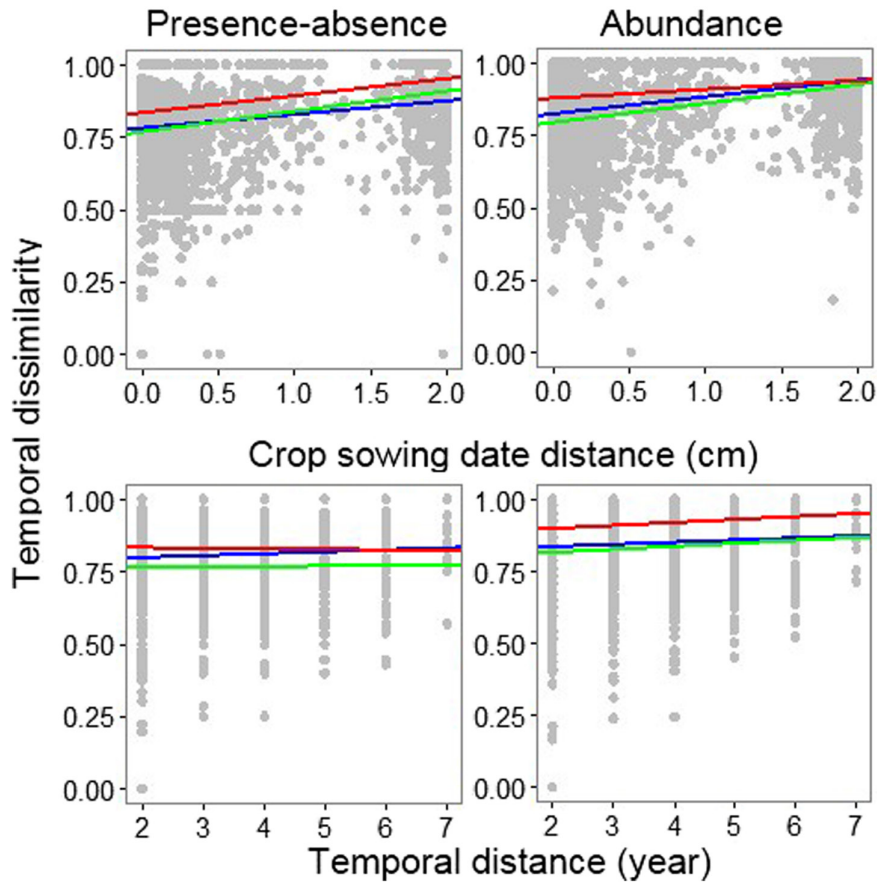
Figure 3. Relationships between temporal weed community dissimilarity based on species presence–absence (Jaccard index) and species relative abundance (Bray–Curtis index) and the difference in crop sowing date (patch availability) (A, B) and temporal distance (C, D). Grey points represent data from the T1 control plots. Blue lines are relationships for control plots at the beginning of the cropping season, green lines are relationships for control plots in the middle of the cropping season and red lines are relationships for herbicide sprayed plots in the middle of the cropping season.

Bray–Curtis indices for T2 control plots was mostly due to the temporal variation of the herbicide spectra with both indices increasing with the temporal variation of the herbicide spectra (0.006 ± 0.003, $p = 0.063$ for the Jaccard index and 0.007 ± 0.003, $p = 0.029$ for the Bray–Curtis index, Supplementary material Appendix 1 Table A3–A4). Finally,

Table 2. Model outputs for temporal weed community dissimilarity calculated using presence–absence data (Jaccard index) for control plots at the beginning of the cropping season (T1 control). Estimated values and standard deviations. Bold p-values are less than 0.05.

Factor	Group	Covariate	Estimate	p-value
Contemporary	Patch availability	Sowing date	0.047 ± 0.004	**<0.001**
	Patch suitability	Crop height	0.001 ± 0.005	0.801
		Precipitation	-0.002 ± 0.004	0.61
		conv–min	0.021 ± 0.001	**0.039**
		min–conv	0.043 ± 0.001	**<0.001**
		min–min	0.029 ± 0.001	**0.005**
	Patch availability × Patch suitability	Sowing date × Precipitation	0.010 ± 0.003	**0.003**
		Sowing date × Crop height	0.010 ± 0.004	**0.019**
Temporal	Temporal distance	Temporal distance	0.007 ± 0.003	**0.022**
	Temporal variation	Variation of sowing date	-0.005 ± 0.005	0.364
		Variation of crop height	0.008 ± 0.006	0.174
		Variation of temperature	0.001 ± 0.004	0.925
		Variation of precipitation	-0.002 ± 0.005	0.638
		Variation of sowing date × Variation of crop height	-0.013 ± 0.004	**0.003**
	Temporal distance × Temporal variation	Temporal distance × Variation of precipitation	-0.007 ± 0.003	**0.029**
Contemporary × Temporal	Patch suitability × Temporal variation	Crop height × Variation of temperature	0.009 ± 0.004	**0.017**

Table 3. Model outputs for temporal weed community dissimilarity calculated using abundance data (Bray–Curtis index) for control plots at the beginning of the cropping season (T1 control). Estimated values and standard deviations. Bold p-values are less than 0.05.

Factor	Group	Covariate	Estimate ± SD	p-value
Contemporary	Patch availability	Sowing date	0.061 ± 0.005	**< 0.001**
	Patch suitability	Temperature	−0.014 ± 0.005	**0.01**
		conv–min	0.036 ± 0.009	**< 0.001**
		min–conv	0.033 ± 0.003	**0.004**
		min–min	0.035 ± 0.005	**< 0.001**
		Temperature × conv–min	0.004 ± 0.009	0.619
		Temperature × min–conv	0.012 ± 0.010	0.285
		Temperature × min–min	0.021 ± 0.008	**0.005**
	Patch availability × Patch suitability	Sowing date × conv–min	−0.028 ± 0.009	**0.001**
		Sowing date × min–conv	−0.013 ± 0.009	0.203
		Sowing date × min–min	−0.018 ± 0.008	**0.023**
Temporal	Temporal distance	Temporal distance	0.007 ± 0.003	**0.02**
	Temporal variation	Variation of sowing date	−0.004 ± 0.005	0.501
		Variation of crop height	0.007 ± 0.005	0.175
		Variation of precipitation	0.001 ± 0.004	0.806
		Variation of sowing date × Variation of crop height	−0.010 ± 0.004	0.02
Contemporary × Temporal	Patch availability × Temporal variation	Sowing date × Variation of sowing date	0.009 ± 0.004	**0.029**
		Sowing date × Variation of precipitation	0.014 ± 0.004	**< 0.001**

there was an increase in interactions between contemporary and temporal factors for the Jaccard index (about 12%, Fig. 2). This was notably due to a positive interaction between tillage intensity and temporal distance, the positive effect of temporal distance on the Jaccard index being greater for conv–min (0.017 ± 0.008, p = 0.038, Supplementary material Appendix 1 Table A3) and min–min (0.028 ± 0.007, p < 0.001, Supplementary material Appendix 1 Table A3) than for conv–conv tillage.

Herbicide spray strongly reduced the effect of contemporary and temporal factors

We assessed the effect of herbicide sprays on temporal weed community dissimilarity by investigating the effect of contemporary factors, temporal distance, and temporal variation on plots sprayed in the middle of the cropping season (T2 sprayed). The third model had the lowest AIC score for the Jaccard index. However, for the Bray–Curtis index, there was no improvement in the AIC score between the second model and the third model (Supplementary material Appendix 1 Table A2). This indicated that adding temporal variation to the model with contemporary factors and temporal distance did not increase the goodness-of-fit for the Bray–Curtis index. Moreover, the covariates selected had very little effect on the indices, explaining only 9.87% and 6.86% of the explained variance for the Jaccard and Bray–Curtis indices respectively (see marginal R^2 in Fig. 2). Distances in crop sowing dates remained the major factor affecting both Jaccard and Bray–Curtis indexes. For the Jaccard index its contribution was much lower than for T2 control plots, while for the Bray–Curtis index it was higher (Fig. 2). As expected, contemporary factors describing patch suitability had a higher relative effect than for T2 control plots for both indices (Fig. 2). Surprisingly,

herbicide spectrum did not have a significant effect on either the Jaccard index (0.003 ± 0.004, p = 0.455, Supplementary material Appendix 1 Table A3) or the Bray–Curtis index (0.005 ± 0.004, p = 0.231, Supplementary material Appendix 1 Table A4) although there was a positive interaction between distance in herbicide spectrum and distance in total annual precipitation (0.010 ± 0.004, p = 0.015 for the Jaccard index and 0.013 ± 0.004, p = 0.0007 for the Bray–Curtis index, Supplementary material Appendix 1 Table A3–A4). Furthermore, herbicide application removed the effect of tillage intensity on both indices (Supplementary material Appendix 1 Table A3–A4). It did, on the other hand, introduce an interaction between tillage intensity and crop height for the Jaccard index (Fig. 2), the positive effect of distance in crop height being higher for conv–min (0.031 ± 0.014 p = 0.025, Supplementary material Appendix 1 Table A3) and min–min (0.031 ± 0.014, p = 0.026, Supplementary material Appendix 1 Table A3) than for conv–conv. Overall, contemporary factors had a lower contribution to the Jaccard index (about 74%) than for T2 control plots while the contribution was similar for the Bray–Curtis index (84.20%). The contribution of temporal distance remained non-significant for the Jaccard index, while its contribution to the Bray–Curtis index was higher than for the T2 control plots (Fig. 2). Finally, herbicide application introduced an interaction between tillage intensity and temporal distance for the Jaccard index, the positive effect of temporal distance being higher for min–min (0.029 ± 0.009, p = 0.002, Supplementary material Appendix 1 Table A3). It also introduced an interaction between temporal distance and crop sowing date for the Bray–Curtis index, the distance in crop sowing date having less effect as the temporal distance increased (−0.009 ± 0.003, p = 0.006, Supplementary material Appendix 1 Table A4).

Discussion

In this study, we aimed at identifying the relative contribution of contemporary and temporal factors in shaping weed communities in arable fields. Although we considered the major contemporary and temporal factors, a large part of variance in the temporal weed community dissimilarity (Jaccard and Bray–Curtis indices) were not explained by these (fixed) effects taken into account, suggesting that other processes can be important in shaping annual weed community assemblies (discussed below). Within the part of explained variance, our results demonstrated that the effect of contemporary factors is about four times higher than the effect of temporal factors. Among contemporary factors, sowing date, which is related to patch availability, had the strongest effect on the weed community assemblies. In the absence of herbicide, the tillage intensity also exerted strong influence on the weed community assemblies, being involved in complex interactions with other factors. Surprisingly, patch suitability covariates, temporal distance and temporal variation individually had a much lower effect on the weed community assemblies. The marginal effect of temporal distance (maximum 5% with $R^2 = 0.19$) suggests that temporal dispersal limitations had little effect on the composition of weed communities, reflecting the ability of many weeds to remain highly persistent in the seed bank, at least over periods up to eight years as covered by the present study. Similarly, past conditions (temporal variation) only had a major effect on the weed community composition at the beginning of the cropping season, suggesting that the main effect of temporal dispersal was to shape weed communities for a short period after patch creation. Additionally, significant two-way interactions between contemporary factors and temporal environmental variation supported the hypothesis that contemporary and temporal processes interact in shaping weed community assemblies.

Weed community assemblies are shaped by patch dynamics and temporal dispersal

By dissociating contemporary factors into patch availability and patch suitability, our results highlight that the difference in patch availability (crop sowing date) is the principal factor explaining weed community temporal dissimilarity. Previous studies have already reported the dominant effect of crop sowing date on weed community taxonomic (Fried et al. 2008, Seifert et al. 2015) and functional (Gunton et al. 2011, Fried et al. 2015, Perronne et al. 2015) composition, invoking the existence of spring, summer, autumn or season-indifferent weed germinating species (Crawley 2004). The high contribution of the crop sowing date to explaining temporal weed community dissimilarity supports studies showing that patch dynamics are important in shaping community assemblages in ephemeral habitat (White and Pickett 1985, Leibold et al. 2004). Also, the decreasing effect of temporal variation and temporal distance through the cropping season support studies showing that community assemblies in ephemeral habitats

depend strongly on species colonization at the time the patch is created (Kim and DeWreede 1996). Dispersal processes may therefore dominate immediately after a disturbance to allow newly created habitats to be colonized (Connell 1978). The increase in the model explanatory power *(*marginal R^2) between the beginning and the middle of the cropping season support this theoretical expectation. Moreover, the temporal distance decays in weed communities growing in the same field in different cropping seasons were weak. This shows that, for the study period (up to eight years), weed community assembly was weakly limited by temporal dispersal, which is consistent with long weed seed persistence in the soil, which is often up to 20 years (Lewis 1973). The effect of the difference in patch suitability on the Bray–Curtis index increased through the cropping season, notably mediated by an interaction between crop height and annual climatic conditions. Since plant height is known to be a proxy of plant species competitive ability for light (Violle et al. 2009), this suggests an increase in competition between crop and weeds over the cropping season, mediated by climatic conditions. This is in agreement with a previous study investigating macrophyte community assemblies in temporary ponds, which showed that interspecific competition was a fundamental ecological driver which interacted with environmental filtering to shape the community assembly over time (Ferreira et al. 2015). After the initial colonization, environmental filtering and biotic interaction should become gradually more important and drive the relative abundance of the species (Boulangeat et al. 2012). We suggest that weed community assemblies are shaped by interaction between the patch dynamics and environmental filtering. The mechanisms affecting weed community assemblies in a given cropping season may be result in a kind of a temporal source–sink dynamics (Holt 1993) acting at the temporal metacommunity scale with the seed bank acting as a source of weed species for weed communities.

Management practices decrease the importance of ecological drivers in structuring weed assembly

In this study, we investigated the effects of two major agricultural practices on weed species assemblies: tillage and herbicide application. Our results revealed different types of effects for these two factors: herbicide application was shown to directly affect weed diversity during cropping season, while tillage notably modified the importance of patch availability and temporal factors (both temporal distance and temporal variation). These findings suggest that herbicides tend to modify weed species assembly during the cropping season, while tillage affects the structure and composition of the seed bank (i.e. availability of species in the local species pool).

Tillage was the main patch suitability factor affecting the weed community temporal dissimilarity. There was a higher effect on weed temporal dissimilarity as well as stronger temporal distance decay for the weed community assembly when minimum tillage was used in both cropping seasons. This agrees with current knowledge of the effect of tillage systems on the soil structure. Minimum tillage does not modify the

structure of the soil and so newly produced seeds remain in the upper layer of the topsoil. Moldboard plowing, however, strongly modifies the soil structure by shearing and displacing the soil (Roger-Estrade et al. 2004). Consequently, old and newly produced seeds are mixed in the topsoil (Colbach et al. 2014) and the soil layers do not represent the temporal history of the crop sequence, buffering the effect of temporal distance. Furthermore, the contribution of patch availability decreased with low-till or no-till practices. Since the tillage date is closely related to the crop sowing date, this suggests that the intensity of a disturbance (tillage depth and soil inversion) when a patch is created may change the effect of patch availability on weed community assemblies.

Herbicide application directly affects the weed community by killing weeds and indirectly modifies the weed community assemblies in the seed bank by promoting the species able to resist the herbicide pressure (species not covered by herbicide spectrum or whose life cycle enables them to escape the treatment), as suggested by the major effect of the temporal variation of the herbicide spectra in both control and sprayed plots. Both temporal weed community dissimilarity indices increased with the temporal variation of the herbicide spectra, suggesting that alternating different herbicidal active ingredients during the cropping season may promote higher weed diversity (Doucet et al. 1999). However, the direct impact of the herbicide spectrum was only detected as an interaction with climatic conditions. This would suggest that herbicide efficiency varies strongly with climatic conditions, in particularly precipitation (Jursík et al. 2013). Moreover, in sprayed plots, herbicide application increased the effect of temporal distance, particularly on the Bray–Curtis index, and decreased the explanatory power of the model (marginal $R^2 = 0.069$ in T2 sprayed and marginal $R^2 = 0.20$ in T2 control). By releasing space and resources, herbicide applications may increase the opportunity for weed species to recolonize after a treatment, increasing the contribution of dispersal-based processes on weed community assembly (Fried et al. 2012).

Spatial dispersal and founder effects may affect weed assembly

Our findings suggest that weed species assemblies at field scale are shaped by interaction between patch dynamics and environmental filtering. However, a large part of the variance (between 93% and 80%) in the temporal weed community dissimilarity remained unexplained by the fixed effects taken into account. A non-negligible part of this variance (about 20%) was explained by random effects in our models showing that idiosyncratic field characters such as farmer's behavior, the long term history of the field (legacy effect) or both, are important in shaping community assemblies. Indeed, Ryan et al. (2010) reported that the signal of a past weed expansion was detected ten years later, suggesting that the local species pool confers a strong inertia to weed assemblies. Nevertheless, about sixty percent of variance in temporal weed community dissimilarity remains unexplained, suggesting that other

processes can be important in shaping annual weed community assemblies. Although quite surprising, low explanatory power seems frequent when analyzing weed communities using large scale datasets (e.g. from 60% to 80% unexplained variance in Pysek et al. 2006; 75% in Pinke et al. 2012). In this study, we assumed that the persistence of weed species in highly dynamic and ephemeral habitats relies on a single strategy based on temporal dispersal, i.e. long persistence in the seed bank. However, the persistence of weed species may be the result of two different strategies, both relying on storage effect (Chesson 2000), as recently proposed by Henckel et al. (2015). The first, as assumed here is a temporal storage effect where species with long persistence in the seed bank can respond to temporal variations in habitats. The second is spatial storage effect which relies on the ability of species to disperse spatially to cope with spatial environmental variations. It is, therefore, very likely that part of the unexplained variance observed here is partly due to spatial colonization from adjacent fields. Another explanation would be that part of this variance is due to differential founder effects across the crop sequence (Levin 1974). These differential founder effects may occur either because not all species reach suitable habitats, or because the sequence of species arrival may have a strong effect on the community composition (priority effects, Fukami et al. 2015). Therefore, the respective roles of temporal dispersal, within and between cropping seasons, as well as spatial dispersal must be disentangled to understand weed assemblies in ephemeral habitat patch mosaics such as agricultural land.

Conclusions

Our analysis emphasizes the critical importance of patch dynamics, environmental filtering and temporal dispersal in shaping the weed community assembly in ephemeral habitats, such as agricultural land. We have shown that temporal dispersal between communities through a crop sequence can allow species persistence through a source-sink effect. In this temporal metacommunity, the seed bank acts as a source of propagules from which weed species having a synchronous life cycle with the patch availability may colonize this ephemeral patch. After colonization, some of these weed species are filtered out regarding to patch suitability making cropping season a sink compartment. Disturbance caused by tillage and herbicide application modify ecological processes by affecting the seed bank structure and composition and by favoring species colonization. However, others processes such as spatial dispersal and founder effects may also profoundly contribute to weed community assembly.

References

Anderson, R. L. et al. 2007. Weed community response to crop rotations in western South Dakota. – Weed Technol. 21: 131–135.

Belsley, D. et al. 1980. Regression diagnostics: identifying influential data and sources of collinearity. – Wiley.

Boulangeat, I. et al. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. – Ecol. Lett. 15: 584–593.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. – Annu. Rev. Ecol. Syst. 31: 343–366.

Crawley, M. J. 2004. Timing of disturbance and coexistence in a species-rich ruderal plant community. – Ecology 85: 3277–3288.

Colbach, N. et al. 2014. Predictive modelling of weed seed movement in response to superficial tillage tools. – Soil Tillage Res. 138: 1–8.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs – Science 199: 1302–1310.

Davison, A. C. and Kuonen, D. 2002. An introduction to the bootstrap with applications in R. – Stat. Comput. Graphics 13: 6–11.

DiCiccio, T. J. and Efron, B. 1996. Bootstrap confidence intervals. – Stat. Sci. 11: 189–212

Ding, D. et al. 2016. Impact assessment of climate change and later-maturing cultivars on winter wheat growth and soil water deficit on the Loess Plateau of China. – Clim. Change 138: 157–171.

Doucet, C. et al. 1999. Separating the effects of crop rotation from weed management on weed density and diversity. – Weed Sci. 47: 729–735.

Falahati-Anbaran, M. et al. 2014. Seed dispersal in time can counteract the effect of gene flow between natural populations of *Arabidopsis thaliana*. – New Phytol. 202: 1043–1054.

Ferreira, F. S. et al. 2015. Spatiotemporal ecological drivers of an aquatic plant community in a temporary tropical pool. – J. Arid Environ. 115: 66–72.

Fried, G. et al. 2008. Environmental and management factors determining weed species composition and diversity in France. – Agric. Ecosyst. Environ. 128: 68–76.

Fried, G. et al. 2012. Trajectories of weed communities explained by traits associated with species' response to management practices. – Agric. Ecosyst. Environ. 158: 147–155.

Fried, G. et al. 2015. Weed flora shifts and specialisation in winter oilseed rape in France. – Weed Res. 55: 514–524.

Fox, J. and Weisberg, S. 2011. An {R} companion to applied regression, 2nd edn. – Sage.

Fukami, T. et al. 2015. Historical contingency in community assembly: integrating niches, species pools and priority effect. – Annu. Rev. Ecol. Evol. Syst. 46: 1–23.

Garamszegi, L. Z. 2011. Information-theoretic approaches to statistical analysis in behavioural ecology: an introduction. – Behav. Ecol. Sociobiol. 65: 1–11.

Ginot, V. et al. 2006. Combined use of local and ANOVA-based global sensitivity analyses for the investigation of a stochastic dynamic model: application to the case study of an individual-based model of a fish population. – Ecol. Model. 193: 479–491.

Gotelli, N. J. and MacCabe, D. J. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. – Ecology 83: 2091–2096.

Gunton, R. M. et al. 2011. Functional traits relating arable weed communities to crop characteristics. – J. Veg. Sci. 22: 541–550.

Gurevitch, J. L. L. et al. 1992. A meta-analysis of field experiment on competition. – Am. Nat. 140: 539–572.

Heap, I. H. 2006. – <www.weedscience.com>.

Henckel, L. et al. 2015. Organic fields sustain weed metacommunity dynamics in farmland landscapes. – Proc. R. Soc. B 282: 20150002.

Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. – In: Species diversity in ecological communities. Univ. of Chicago Press. pp. 77–88.

Horn, H. S. and MacArthur, R. H. 1972. Competition among fugitive species in a harlequin environment. – Ecology 53: 749–752.

Hyvönen, T. and Salonen, J. 2002. Weed species diversity and community composition in cropping practices at two intensity levels – a six-year experiment. – Plant Ecol. 154: 73–81.

Jeffries, M. J. 2008. The spatial and temporal heterogeneity of macrophyte communities in thirty small, temporary ponds over a period of ten years. – Ecography 31: 765–775.

Jeffries, M. J. 2011. The temporal dynamics of temporary pond macroinvertebrate communities over a 10-year period. – Hydrobiologia 661: 391–405.

Jursík, M. et al. 2013. Effect of precipitation on the dissipation, efficacy and selectivity of three chloroacetamide herbicides in sunflower. – Plant Soil Environ. 59: 175–182.

Kim, J. H. and DeWreede, R. E. 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. – Mar. Ecol. Prog. Ser. 133: 217–228.

Kuznetsovat, A. et al. 2015. lmerTest: tests in linear mixed effects models. – R package ver. 2.0-33. <https://CRAN.Rproject.org/package=lmerTest>.

Leibold, M. A. and Loeuille, N. 2015. Species sorting and patch dynamics in harlequin metacommunities affect the relative importance of environment and space. – Ecology 96: 3227–3233.

Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – Ecol. Lett. 7: 601–613.

Levin, S. A. 1974. Dispersion and population interactions. – Am. Nat. 108: 207–228.

Lewis, J. 1973. Longevity of crop and weed seeds: survival after 20 years in soil. – Weed Res. 13: 179–191.

Mahaut, L. et al. 2017. Data from: Patch dynamics and temporal dispersal partly shape annual plant communities in ephemeral habitat patches. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.5q114>.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.

Nekola, J. C. and White, P. S. 1999. The distance decay of similarity in biogeography and ecology. – J. Biogeogr. 26: 867–878.

O'Brien, R. O. 2007. A caution regarding rules of thumb for variance inflation factors – Quality Quantity. 41: 673–690.

Oksanen, J. F. et al. 2015. Vegan: community ecology package. – R package ver. 2.4-3. <https://CRAN.R-project.org/package=vegan>.

Perronne, R. et al. 2015. Stochastic processes and crop types shape weed community assembly in arable fields. – J. Veg. Sci. 26: 348–359.

Pinke, G. et al. 2012. The influence of environment, management and site context on sepcies composition of summer arable vegetation in Hungary. – Appl. Veg. Sci. 15: 136–144.

Pysek, P. et al. 2006. Effects of abiotic factors on species richness and cover in central European weed communities. – Agric. Ecosyst. Environ. 109: 1–8.

Reigada, C. et al. 2015. Metapopulation dynamics on ephemeral patches. – Am. Nat. 185: 183–195.

Roger-Estrade J. et al. 2004. Morphological characterization of soil structure in tilled fields. From a diagnosis method to the modelling of structural changes in tilled soils over time. – Soil Tillage Res. 79: 33–49.

Ryan, M. R. et al. 2010. Management filters and species traits: weed community assembly in long-term organic and conventional systems. – Weed Sci. 58: 265–277.

Seifert, C. et al. 2015. Arable plant diversity on conventional cropland – the role of crop species, management and environment. – Agric. Ecosyst. Environ. 213: 151–163.

Venable, D. L. 2007. Bet hedging in a guild of desert annuals. – Ecology 88: 1086–1090.

Violle, C. et al. 2009. Competition, traits and resource depletion in plant communities. – Oecologia 160: 747–755.

Weiner, J. et al. 2010. Evolutionary agroecology: the potential for cooperative, high density, weed-suppressing cereals. – Evol. Appl. 3: 473–479.

Pickett, S. T. A. and White, P. S. 1985. Natural disturbance and patch dynamics: an introduction. – In: The ecology of natural disturbance and patch dynamics. Elsevier, pp. 3–13.

Supplementary material (available online as Appendix oik-04415 at <www.oikosjournal.org/appendix/oik-04415>). Appendix 1–3.