Long-term farming systems and last crop sown shape the species and functional composition of the arable weed seedbank

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Abstract

Questions

The assembly of arable weed communities is the result of local filtering by agricultural management and crop competition. Therefore, soil seedbanks can reflect the effects of long-term cumulative field management and crop sequences on weed communities. Moreover, soil seedbanks provide strong estimates of future weed problems but also of potential arable plant diversity and associated ecological functions. For this, we evaluated the effects of different long-term farming systems under the same crop rotation sequence on the abundance, diversity and community assembly of weed seedbank, as well as on the functional diversity and composition.

Location

DOK (biodynamic (D), bioorganic (O), conventional (K)) long-term trial, Therwil, Switzerland.

Methods

The effects of long-term contrasted farming systems (i.e., biodynamic, organic, conventional, mineral and unfertilised systems) and last crop sown (i.e., wheat and maize) were evaluated on different indicators of species and functional diversity and composition of the weed soil seedbank.

Results

The results showed significant influences of 40-years of contrasted farming systems on the diversity and composition of the seedbank, with higher diversities being found in unfertilised and organic farming systems, but also higher abundances than those found under conventional systems. Organic farming also allowed higher functional richness, dispersion and redundancy. Different farming systems triggered shifts in species and functional assemblies.

Conclusions

The results highlight the importance of organic management for the maintenance of a diverse arable plant community and its functions. However, such results emphasize the need for appropriate yearly management to reduce the abundance of settled weediness and prevent affecting crop production. The farm management filtered community composition based on functional traits. Although the soil seedbank buffers the long-term farming and crop sequence, the last crop sown and, thus, the yearly management were important determinants of seedbank composition.

Keywords

Arable farming, conventional farming system, crop type, functional diversity and redundancy, long-term management, organic farming system, soil seedbank, species abundance and diversity, weeds

1. Introduction

Management of agricultural land has largely focused on weed control to reduce the abundance of undesired species and prevent crop losses. However, these practices have resulted in a widespread decline of arable weed diversity (Baessler & Klotz, 2006; Preston et al., 2002) to the point of being a matter of concern because, apart from their intrinsic conservation value, weeds have an important ecological function delivering ecosystem services such as contributing to soil structuring or as key components in the food webs of agroecosystems (Hawes et al., 2003; Marshall et al., 2003).

The assembly of weed communities responds to local filtering processes, which are mainly the farming practices and the competition exerted by crops. Weeds are thus suitable indicators of agricultural intensity because they have high sensitivity to farming practices (Rotchés-Ribalta, Blanco-Moreno, Armengot, Chamorro, & Sans, 2015) and are strongly related to other organism groups (Marshall et al., 2003). Nevertheless, the weed seedbank might be a more reliable indicator of the effects of long-term management and cropping sequence than the aboveground weed community because the seedbank is the result of cumulative processes that occurred in the past (Albrecht & Auerswald, 2009; Hawes, Squire, Hallett, Watson, & Young, 2010) and consequently, it could better reflect the effect of agricultural practices and cropping systems over the years. Furthermore, seedbank analysis may allow overcoming differences due to management in the sampling year with regards to weed control effectiveness or cropping practices of a given year, according to Bohan et al. (2011).

Less intensive farming systems, such as organic systems, have been usually associated with higher species diversities in comparison to conventional farming systems, which are characterised by the use of synthetic chemical fertilisers, pesticides and herbicides, intensive tillage and high sowing densities, among others. Besides, organic farming have also been reported to enhance species richness in the seedbank (Albrecht, 2005; Menalled, Gross, & Hammond, 2001; Rotchés-Ribalta, Armengot, Mäder, Mayer, & Sans, 2017), as well as the seedbank size relative to conventional systems (Hawes et al., 2010; Ryan, Smith, Mirsky, Mortensen, & Seidel, 2010). However, a lack of effect of farming systems on seedbank size and diversity has also been described (Dölle & Schmidt, 2009; Sjursen, 2001). These different results could be largely attributed to heterogeneity within each farming system and to methodological shortcomings, such as differences in the spatial scale at which the studies were conducted (Bengtsson, Ahnström, & Weibull, 2005). Farming systems (i.e. organic or conventional management) are usually associated with specific agricultural practices such as crop rotation or the type of soil tillage, making it difficult to fully understand the patterns of these different practices. For this, trials under controlled conditions allow discernment between the effects of specific parameters and better understand the underlying processes shaping weed communities. Moreover, trials run for long-term periods can provide valuable knowledge on the effects of agricultural practices on the weed seedbank community assemblies (Albrecht & Auerswald, 2009).

The effects of long-term contrasted farming systems on weed seedbank size and diversity have been previously addressed (e.g. Albrecht & Auerswald (2009); Menalled et al. (2001); Rotchés-Ribalta et al. (2017)). However, species diversity indices can only reflect parts of the complexity of weed communities and thus the effects of farm management on weed communities cannot be captured by a single diversity index but need to be documented through in-depth analysis of floristic composition and community functional attributes. The species composition of weed seedbank represents a good indicator of trends in diversity because they are the result of non-random filtering of the local species pool by farm management and cropping history, especially at larger temporal scales (Hawes et al., 2010; Menalled et al., 2001). These assemblages are determined by the functional attributes that the species possess (Perronne, Le Corre, Bretagnolle, & Gaba, 2015; Solé-Senan, Juárez-Escario, Conesa, & Recasens, 2018) and, thus, the consideration of functional diversity descriptors of the soil seedbank may be a reliable estimate of the long-term effects of contrasted farming. Besides, the soil seedbank can hold similar levels of functional diversities as the aboveground vegetation

(Pakeman & Eastwood, 2013), and thus, the functional approach of the seedbank can be a promising and novel way to understand weed community assembly after long-term management effects (Gaba, Fried, Kazakou, Chauvel, & Navas, 2014; Navas, 2012). Therefore, consideration of not only the species diversity indices but also the functional descriptors of the community is important to fully understand the patterns of long-term farming systems in shaping the seedbank and thus, of potential established weed community. Given the importance of functional diversity and redundancy to ecosystem resilience (Laliberté et al., 2010), an assessment of the impacts of long-term farm management on these indices is crucial to determine the vulnerability of functional groups to future perturbations (Laliberté et al., 2010).

The aim of this study was to evaluate the effects of long-term farming systems and last crop sown (as a proxy of yearly cropping practices) on the abundance, diversity, and community assembly of the soil seedbank, as well as on the functional diversities and composition. The study was carried out in wheat and maize crops under organic and conventional farming systems within a replicated, long-term experiment [DOK: biodynamic (D), bioorganic (O), conventional (K) trial, Therwil, Switzerland]. Although plot-scale studies have been questioned because the population dynamics of many organisms operate at larger scales (Bengtsson et al., 2005), the importance of this study in the DOK trial lies in the accurate monitoring of farming practices of each farming system, which have been under the same crop rotation scheme, and homogeneity among plots within each system, which were rare in previous studies (Menalled et al., 2001; Squire, Rodger, & Wright, 2000). The effects of farming on crop yields, soil fertility and biodiversity of different groups of organisms (e.g., earthworms, arthropods and aboveground weeds) in the DOK trial have already been analysed by Fließbach, Oberholzer, Gunst, & Mäder (2007) and Mäder et al. (2002), among others. However, little attention has been paid to the effects of long-term farming practices of the DOK trial on the soil seedbank (except for Rotchés-Ribalta et al. (2017)) and on its specific and functional composition, although knowledge on seedbanks might be indicative of long-time scale effects.

For this reason, in the current study, we aimed to complement the previous study conducted on one single crop type (Rotchés-Ribalta et al., 2017) and answer: 1) whether long-term contrasted farming systems and the last crop sown affect weed abundance, species diversity, and its two components species richness and evenness, of the soil seedbank; 2) whether farming system and crop type affect the weed species assemblies of the seedbank; and 3) whether the functional diversity and the functional composition of the seedbank respond to long-term farming practices and the last crop sown. Overall, we assumed that the size and the diversity of the weed seedbank were lower in conventional than in organic systems because of the high pressure of farming practices. We also expected that the different farming systems would result in a different community assembly because of the different tolerance and response of each particular species to management intensity. We specifically expected higher functional diversity and redundancy under less-intensified farming systems. Furthermore, we expected to find more competitive species, better adapted to more intensive weed control and high nutrient availability (e.g., taller plants with higher SLA and larger seeds) in conventional farming systems. Contrarily, given that soil seedbanks reflect the long-term effects and that crop rotation in the DOK long-term trial has been the same in all plots, we did not expect a great effect from the last sown crop on the soil seedbank.

2. Methods

2.1. Study site

The study was conducted in the DOK long-term agricultural experiment of Therwil, Switzerland (7º33'E, 47º30'N), which compares biodynamic (D), bioorganic (O) and conventional (K) farming systems. Detailed information on the DOK trial is given by Mäder et al. (2002). The climate of the site is characterised by a mean annual temperature of 9.5ºC and an annual precipitation sum of 785mm.

2.2. Experimental design and farm management

The sampling was carried out in 2009 in wheat and maize plots that were under five different farming systems: two conventional (i.e., conventional (hereafter CONFYM) and mineral (CONMIN)), two organic (i.e., organic (BIOORG) and biodynamic (BIODYN)) and an unfertilised (NOFERT) farming systems since 1978. The 5m × 20m plots under each farming system and crop were randomly placed within four blocks (replicates) in a randomised split-split-plot design that covered approximately 1.5 hectares (Figure 1). Crop rotation and soil tillage were identical in the five farming systems. The 7-year rotation included series of potatoes, winter wheat, soybeans, maize, winter wheat, grass-clover and grass-clover (Table S1.1 in Supplementary Materials). In 2009, the crops were maize, winter wheat and potato.

Different fertilisation regimes and plant protection strategies characterised these systems (Table S1.2 in Supplementary Materials). Farmyard manure and slurry corresponding to 1.2 (1st and 2nd rotation period) and 1.4 (3rd rotation period) livestock units/ha were applied in the organic systems (BIOORG and BIODYN). BIOORG plots were also fertilised with small amounts of rock dust and potassium magnesia. CONFYM system was fertilised with the same amount of farmyard manure and with mineral fertilisers up to recommended levels from the Swiss standards. CONMIN plots were amended with mineral fertilisers exclusively (from the 2nd crop rotation onwards). The level of fertilisation increased gradually from NOFERT, BIODYN, BIOORG to CONFYM and CONMIN, corresponding to 0kg N ha^{-1} in NOFERT; 95kg N_t ha^{-1} and 26kg N_{min} ha^{-1} (being N_t the total nitrogen content and N_{min} the mineral nitrogen) in BIODYN; 98kg N_t ha^{-1} and 31kg N_{min} ha^{-1} in BIOORG; 170kg N_t ha^{-1} and 111kg N_{min} ha^{-1} in CONFYM; and 122kg N_t ha^{-1} and 122kg N_{min} ha^{-1} in CONMIN farming systems, during the 3rd rotation period (when 1.4 livestock units/ha were applied).

Organic and conventional systems also differed in terms of plant protection strategies (Table S1.2). Weed control in organic and in unfertilised systems was performed only mechanically (i.e., through seedbed preparation, post-emergence control or manually), whereas chemical weed control, apart from the mechanical, was carried out in conventional systems. Plant extracts and preparations were used to protect plants in BIODYN and BIOORG systems, while fungicides and insecticides based on threshold values were used in CONFYM and CONMIN systems (see Table S1.2 for details).

2.3. Sampling

Sampling took place in five DOK systems (NOFERT, BIODYN, BIOORG, CONFYN and CONMIN) after maize and wheat crops in September 2009. The soil seedbank in the potato crops was sampled in June 2009, while the crop was still standing, which is why results from the potato crop seedbank were presented in a separate study (Rotchés-Ribalta et al., 2017). Soil samples were collected with an auger from the inner 12m × 3m of each plot (to avoid edge effects) to a depth of 20cm and a core of 2.8cm in diameter (Figure 1). The sampling was performed on a 0.75m × 2m grid pattern, resulting in 35 soil samples per plot (Figure 1). From these 35 soil samples, a group of seven samples was each evenly distributed in a shallow aluminium tray (28.5 × 18.6 cm, Figure 1), obtaining a total of five trays per plot. Trays were placed in a non-heated greenhouse bench under natural photoperiod and watered regularly (Faculty of Biology, University of Barcelona). The position of the trays was changed randomly every 3-4 weeks. Samples were periodically allowed to dry mildly, and they were turned, aerated, and watered again to stimulate germination. A detailed description of the method is given by Gibson (2002). Emerged seedlings were periodically identified and removed after counting. Taxonomic nomenclature followed Tutin (1993). Seedling inventories were conducted thirteen times during a period of November 2009 to December 2010.

2.4. Diversity indices

The number of weed species in the seedbank within each farming system and crop type was obtained from the list of species of all sampling dates in each aluminium tray. The abundance, assessed as the number of seedlings m^{-2} of field for each species, was calculated by dividing the total number of seedlings emerged in each aluminium tray by the total area of soil cores collected in the field and grouped in each tray ($[(0.014)^2\times\pi]\times7$).

The diversity of the weed seedbank was split into the following parameters calculated for each tray (Magurran, 2004): a) species richness (*s*), as number of species per tray; b) Shannon's diversity index (*H'*); and c) Pielou's evenness index (*J'*). Despite some indices might be correlated (Dejong, 1975), they allowed us to capture different aspects of diversity and better quantify the concept.

The effects of farming system and crop type on seedbank abundance, species richness, diversity and evenness were analysed by linear mixed-effects models (Pinheiro & Bates, 2000), with the inclusion of the nested sampling design of random factors (crop sub-sub-block nested to treatment sub-block and this, nested to block; trays were considered pseudo-replicates). Normality of the data and homogeneity of variances were checked visually and tested using the Shapiro-Wilk and the Levene test, respectively. Abundance and species richness were log-transformed to comply with assumptions of normality and homoscedasticity. Orthogonal contrasts were performed to compare between NOFERT and the other fertilised treatments, between the organic systems (BIOORG and BIODYN) and the conventional ones (CONFYM and CONMIN), between BIODYN and BIOORG, between CONFYM and CONMIN and between Wheat and Maize. Statistical analysis were conducted under R 3.6.0 (R Core Team, 2016), using "lme4" (Bates, Mächler, Bolker, & Walker, 2015) for mixed-effects models and "lmerTest" for evaluating the P-values (Kuznetsova, Brockhoff, & Christensen, 2017).

2.5. Seedbank composition analysis

A multivariate analysis using presence/absence data of species was conducted to assess the species composition of the seedbank under the different farming systems and crop types. Species that occurred only in one tray were eliminated because they did not add information for the ordination. The Jaccard dissimilarity index was computed between the lists of species (47 species) of each farming system and crop combination. Since we used a non-Euclidean distance metric, we chose non-Metric Multidimensional Scaling (NMDS) for this ordination, using a stable solution by random starts with k = 2 dimensions. NMDS is a robust unconstrained ordination method in community ecology (Minchin, 1987), and restricting the number of dimensions to two facilitates the graphical representation while achieving fairly good stress (0.146). Farming system and crop type were fitted onto the ordination, and their significance was tested with random permutations of the data. Species with more than 20% of the total presence were also fitted onto the ordination. We carried out this analysis under R 3.6.0 (R Core Team, 2016) using the 'vegan' package (Oksanen et al., 2019).

2.6. Functional analysis

Functional diversity components (functional richness, functional evenness and functional dispersion) were computed based on the multiple trait matrix (Table 1) of arable species recorded in each farming system and crop type using the FD package (Laliberté, Legendre, & Shipley, 2014) for R 3.6.0 (R Core Team, 2016). With this package, a Principal Components Analysis (PCA) was performed based on the Gower dissimilarity matrix, as calculated for the species by traits matrices. The obtained axes were then used to compute functional richness and functional evenness. Functional richness expressed the multidimensional trait space occupied by species in each community. Functional evenness quantified how even individuals from a community are distributed over trait space. Functional dispersion was computed based on the trait dispersion per community considering the relative abundances (Laliberté et al., 2014). The multiple trait matrix was also used to calculate functional redundancy of seedbank species per farming system and crop type using the SYNCSA package (Debastiani, 2018) for R 3.6.0 (R Core Team, 2016). Functional redundancy was calculated as the difference between the species diversity and Rao's quadratic entropy based on their functional dissimilarity.

Plant functional traits and types were selected based on literature relative to the functional responses to management and potential interference with crop (Bàrberi et al., 2018). The traits and types included in the functional diversities computation were the Raunkiær life form (categorical), growth form (categorical), soil seedbank longevity (proportion reported in each category: long-term, short term and transient), specific leaf area (SLA, numerical), plant canopy height (numerical), seed weight (numerical), affinity to nutrient conditions (numerical) and seasonality of germination (proportion of chances to germinate in each season) (Table 1). Most of the trait and type information for each species was obtained from Bàrberi et al. (2018, Appendix S1) or, for species not present in this database, from literature following the same criteria. Size measures (i.e., plant height, SLA and seed weight) were log-transformed to homogenise the weight across taxa before calculation. Given that seedbank longevity was entered as proportion reported in each category and seasonality of germination as proportion of chances to germinate in each season, each category of seedbank longevity was weighted by 0.33, and each season of germination was weighted by 0.25, for an overall contribution of each functional trait of 1.

The effects of the farming system and crop type on the functional diversity indices of the weed seedbank communities were analysed using the same linear mixed-effects model framework as for the analyses of diversity indices (see section “2.4. Diversity indices”).

Besides, we estimated the composition of functional traits and types using the community-weighted mean (CWM) from the multi-trait matrix using the FD package (Laliberté et al., 2014) for R 3.6.0 (R Core Team, 2016). Given that CWM has negative values, the ordination of samples according to functional composition was conducted by means of a PCA. The CWM trait matrix was used to perform a PCA to produce orthogonal axes of functional trait composition and reduce trait redundancy. The first two axes obtained were used to plot the seedbank samples of each farming system and crop type according to their functional trait composition values. The significance of these two first PCA axes on spreading the samples according to farming system and crop type was analysed using the same linear mixed-effects models (Pinheiro & Bates, 2000) used for the diversity indices analyses (see section: “2.4.

Diversity indices”). These models were also used to assess the effects of farming system and crop type on the CWM values of each trait/type or trait level of the weed seedbank community.

3. Results

3.1. Overview

A total of 20,362 seedlings were counted, corresponding to 50 species. Thirty-seven and 33 of these appeared in CONFYM and CONMIN systems respectively; 40 and 42 were found in the BIOORG and BIODYN systems, respectively; and 44 species were counted in NOFERT system. While 32 species were recorded in all farming systems, only three species were detected only in the BIOORG and BIODYN plots, and one in the two conventional systems (CONFYM and CONMIN). Mean seedbank density values varied between farming systems. While 6,195 and 8,404 seedlings m^{-2} were found in the CONFYM and CONMIN systems respectively, 19,622 and 14,413 seedlings m^{-2} were found in the BIOORG and BIODYN systems. In the NOFERT system, the seedbank density was 69,468 seedlings m^{-2}. Species with highest relative density in all farming systems were *Sagina procumbens, Chenopodium polyspermum, Juncus bufonius* and *Poa annua*. Several species showed different abundance patterns between long-term farming systems and crop types (Table S1.3 in Supplementary Materials).

3.2. Seedbank density and diversity

The NOFERT system held significantly greater seedbank density than the fertilised systems (Figure 2; Table 2). The seedbank density in the organic (BIOORG and BIODYN) farming systems was significantly greater than in the conventional (CONFYM and CONMIN) farming systems and in BIOORG compared to BIODYN (Figure 2; Table 2). A similar pattern was found for species richness, with higher values in the NOFERT system relative to the other fertilised systems and in organic (BIOORG and BIODYN) compared with conventional systems (CONFYM and CONMIN) (Figure 2; Table 2). The Shannon diversity indices varied between farming systems too with a significantly higher Shannon’s index in the organic farming systems (BIOORG and BIODYN) compared with the conventional systems. Species evenness was significantly higher in the NOFERT system than in the fertilised ones (BIOORG, BIODYN, CONFYM and CONMIN).

Seedling density and species richness did not differ among crop types, except for the NOFERT plots with wheat, which had a higher number of seedlings, as indicated by the significant interaction (Table 2). Significant interactions between crop types and farming systems were also found for seedling evenness: while fertilised wheat crops had higher evenness indices than fertilised maize crops, the opposite was observed in the NOFERT plots (Figure 2; Table 2).

3.3. Seedbank species composition

Farming systems were linked to shifts in the seedbank species composition (NMDS, $k = 2$, non-metric fit: $r^2 = 0.973$); with differences between the NOFERT, organic (BIOORG, BIODYN) and conventional (CONFYM, CONMIN) systems. The fit of farming systems onto the plot differed significantly ($r^2 = 0.273$, $P < 0.001$), indicating a gradient from the conventional towards organic and unfertilised systems (Figure 3.a). Samples also differed according to crop type ($r^2 = 0.062$, $P < 0.001$, Figure 3.b), with species such as *Papaver rhoeas*, *Cardamine hirsuta* or *Chaenorhinum minus* appearing more commonly in wheat crops, and *Amaranthus blitoides* or *Chenopodium polyspermum* occurring more commonly in maize crops (Figure 3.c). The NOFERT system was separated in the ordination by the high presence of *Sagina procumbens*, *Polygonum hydropiper* and *Gnaphalium uliginosum* (Figure 3.c).

3.4. Seedbank functional diversity

Functional richness was significantly higher in the unfertilised system than in the fertilised systems; and significantly higher in the organic farming systems (BIODYN and BIOORG) than in the conventional ones (CONFYM and CONMIN) (Figure 4; Table 2). Likewise, functional evenness was marginally greater in the NOFERT system than in the fertilised ones. However, the NOFERT system presented lower functional dispersion than the fertilised systems, and the organic systems had higher functional redundancy than the conventional ones (Figure 4; Table 2).

Wheat crops showed lower levels of functional richness but higher functional redundancy and functional evenness than maize crops (Figure 4). However, the higher functional redundancy in the wheat crops was specific to fertilised systems (i.e., no differences were found on the functional redundancy between crop types for the unfertilised systems) (Table 2).

3.5. Seedbank functional composition

The first two axes of the PCA run for the seedbank CWM data explained 43.98% and 18.85% of the total variance, respectively (see Table S1.4 in Supplementary Material for the values of the first two PCA axes per trait). The CWM, when used as indicator of functional composition, determined the ordination of seedbank samples according to farming systems, particularly separating the NOFERT system samples from the fertilised ones (Figure 5.A, Table S1.5 in Supplementary material). The crop type also determined a slight separation of the samples according to their functional composition (Figure 5.B, Table S1.5). When representing the levels of functional traits and types considered in the ordination, the NOFERT system was characterised by a higher abundance of hemicryptophytes, rosette-growing plants and short-term seedbank (Figure 5.C). The therophyte life form, higher SLA, seed weight, canopy height and higher nutrient affinity characterised all fertilised plots (Figure 5.C). Wheat crops under the fertilised systems were characterised by graminoid-growing plants with transient seedbanks and autumn-germination, whereas maize crops under fertilised systems were characterised by ascending plants, long-term seedbanks and spring-germinating species (Figure 5.C). See Table S1.6 (Supplementary Materials) for further details on the results of the CWM per trait in response to farming systems and crop type.

4. Discussion

The different long-term farming systems, under the same crop rotation sequence and tillage practices, resulted in significant differences in the seedbank weed community. Although previous studies pointed out to a strong influence of crop rotation and tillage on weed communities (Mahaut, Gaba, & Fried, 2019), here we found that other farming practices determined significant differences in the abundance, diversity and floristic composition of the weed seedbank, as well as in the functional diversity, redundancy and composition. Besides, we found that not only long-term farming but also the yearly management associated to the last crop sown were important determinants of the functional and species composition of the soil seedbank.

4.1. Dominant species

Only a few species showed high relative densities in all farming systems, and these were weeds that produce many small seeds highly persistent in the seedbank or with high dispersal ability, such as *Poa annua* and *Sagina procumbens* (Dölle & Schmidt, 2009). Some species with high relative density in NOFERT system were likely selected by the lack of fertilisation, whereas others with low abundances in NOFERT, such as *Cerastium glomeratum*, require high nutrient availability (De Cauwer, Van Den Berge, Cougnon, Bulcke, & Reheul, 2010). Many of the species that were abundant in conventional systems (e.g., *Chenopodium polyspermum* and *Poa annua*), are nitrophilous species (Ellenberg, Weber, Düll, Wirth, & Werner, 2001), as reported by Hawes et al. (2010) and De Cauwer et al. (2010), responding to the nutrient conditions of those systems (Mäder et al., 2002). The species that are abundant in conventional systems are likely to be resistant or difficult to control with herbicides (Rotchés-Ribalta et al., 2017). In contrast, other arable species that predominate in organic systems, such as *Arabidopsis thaliana*, *Papaver rhoeas* and *Amaranthus lividus*, are more sensitive to chemical weed control and favoured by nutrient availability conditions from organic amendments (De Cauwer et al., 2010; Hawes et al., 2010).

4.2. Seedbank density and diversity

Seedbank density values found in the DOK trial correspond to results obtained in other studies (Hawes et al., 2010; Menalled et al., 2001; Rotchés-Ribalta et al., 2017), with higher densities in the unfertilised system, indicating that lower nutrient availability involved a decrease in the number of seeds incorporated in the soil from established weed populations (De Cauwer et al., 2010). In general, weed seedbank abundance responds positively to fertilisation; nevertheless, when weeds grow in competition with crop, the crop usually has higher competitive ability that negatively affects the reproductive output of weed species (Gaba, Caneill, Nicolardot, Perronne, & Bretagnolle, 2018) and thus the number of seeds shed to the soil. Differences in fertilisation also determined higher species richness in the NOFERT system but also lower species evenness. Therefore, although the lack of fertilisation involved greater species richness in the weed seedbank, it also promoted greater abundance of few species more adapted to the nutrient conditions in this system.

Organic farming, characterised by lower weed management intensity (i.e., conducted only mechanically) and with less nutrient inputs, held a larger seedbank than conventional farming systems, as previously reported (De Cauwer et al., 2010; Rotchés-Ribalta et al., 2017). Established weed populations were, thus, better suppressed by both chemical and mechanical weed controls used in conventional farming systems (Menalled et al., 2001), together with increased indirect effects of crop competition due to higher nutrient availability in conventional systems (Squire et al., 2000). This effect has likely reduced the amount of seeds shed onto the soil. The trend of higher seedbank density in organically managed systems indicates the potential threat these seeds can represent as future weed pests if they germinate and establish in densities exceeding thresholds to compete with crops. However, seedbank communities in organic farming systems also showed higher species diversities than conventional systems, as reported previously (Albrecht, 2005; Rotchés-Ribalta et al., 2017; Ryan et al., 2010). This trend mimics patterns found for aboveground weed vegetation (Mäder et al., 2002) and highlights the potential of seedbank in organic farming systems to guarantee a diverse arable species community (Menalled et al., 2001).

Species evenness in organic and conventional systems did not differ, indicating that all communities, independently of the farming system, held equally abundant species. These results disagreed with previous studies that pointed out that conventional systems tend to hold higher abundances of seeds in the seedbank of only a few species that are tolerant to more intensive farming practices (Dölle & Schmidt, 2009).

The crops investigated, i.e., maize and wheat, held similar levels of seedbank density, species richness and Shannon's diversity index, in accordance with our expectations, as the seedbank represents the integrative response of weed communities to environmental and management conditions over the years (Bohan et al., 2011). However, higher species evenness was found in wheat crops when they were fertilised, indicating a fair difference in the community structure depending on the last crop sown but with different behaviours depending on the fertilisation.

4.3. Seedbank species composition

The distinct floristic composition of the seedbank among farming systems reflected the long-term cumulative effects of 40-years farming, reinforcing trends of previous studies (Hawes et al., 2010; Menalled et al., 2001; Rotchés-Ribalta et al., 2017), and indicating that accumulated farming practices filtered the species with different sensitivity to management intensity.

The seedbank species composition showed differences between the crop types sown, contrary to our expectations. This highlights the significant influence of the weed community established in the previous season, which shed a particular composition of seeds to the soil (Menalled et al., 2001). Such differences are likely to come from differences in the field preparation depending on the time of sowing of each crop, which encourage or inhibit certain species to thrive (Menalled et al., 2001; Perronne et al., 2015).

4.4. Seedbank functional diversity and composition

Farm management filters the community composition of arable species according to functional traits rather than species (Solé-Senan et al., 2018). Therefore, functional diversity indices can be more sensitive to community assembly rules than species diversities (Mouchet, Villéger, Mason, & Mouillot, 2010). However, in our study, the response of functional richness was similar to that of species richness, being higher in less intensified systems (i.e., in NOFERT system compared with fertilised systems and in organic systems compared with conventional ones). Although positive relationships between species richness and functional richness are common, these indices are not surrogates *per se* (Díaz & Cabido, 2001), and therefore, the consideration of different components of biodiversity is important to fully understand the community assemblies in response to long-term farming. Higher functional richness found in NOFERT system and in organic farming systems indicates that these less intensified systems held greater odds that at least some species may respond differently to variable conditions and perturbations (Díaz & Cabido, 2001).

Given that agricultural intensification acts as filter constraining plant species according to their functional traits and ecological strategies, a reduction in farming intensity is usually associated with increased functional divergence (Armengot et al., 2016; Solé-Senan et al., 2018). Our results, however, point to a different pattern, with lower functional dispersion in unfertilised systems in comparison with all the fertilised ones. This highlights that the NOFERT system offered particular conditions and constraints, such as lower nutrient availability and soil organic carbon (Fließbach et al., 2007), which may reduce the space of successful ecological strategies and promote the dominance of a few specific functional traits and types.

Seedbank communities under long-term organic farming showed higher functional redundancy than conventional farming, similar to other studies that attributed negative effects on community stability to management intensity (Laliberté et al., 2010; Pillar et al., 2013). Functional redundancy represents an insurance for the maintenance of ecosystem processes in case of perturbations (Pillar et al., 2013). Therefore, arable weed communities in less-intensive systems will be more stable and resilient whereas weed communities in conventional systems will be more sensitive to disturbance and land-use changes.

Although arable weed species show similar functional attributes as they respond to specific resource acquisition, growth strategies and tolerance to disturbances (Bourgeois et al., 2019), in the current study, we found clear shifts in the mean trait values of seedbank communities depending on the long-term farming systems. The seedbank community in fertilised systems was characterised by traits typically related to better competitive abilities such as high nutrient affinity, higher SLA, canopy height, seed weight and a greater proportion of therophytes. These response attributes are related to weed communities and are indicative of fast life strategies (Bourgeois et al., 2019; Navas, 2012). Fertilisation entails a resource-rich environment selecting plants with high SLA and short life forms such as therophytes (Solé-Senan et al., 2018; Storkey et al., 2013), whereas increases in competition with the crop for resources (i.e., light, nutrients and water) favour species with tall canopies and heavy seeds (Albrecht & Auerswald, 2009; Maclaren, Bennett, & Dehnen-Schmutz, 2019; Storkey et al., 2013). Although plant protection strategies may involve changes on species communities according to functional traits (Maclaren et al., 2019; Solé-Senan et al., 2018), no significant differences were found on mean trait values between seedbank communities of conventional and organic farming systems. Therefore, diverging methods of weed control and fertilisation in the long-term trial did not involve differences on the functional composition of the seedbank.

The functional composition differed depending on the crop sown in the previous season, contrary to our expectation. The last crop sown may have filtered the arable species community through the timing of agricultural operations, selecting those species that germinate and emerge simultaneously with the crop or with phenology mimicking the crop (Bourgeois et al., 2019; Perronne et al., 2015). According to our results, the preceding crop determined a particular weed community that shed seeds to the soil with a specific functional assembly. Hence, the seedbank in wheat crops was characterised by autumn-germinating species, whereas the seedbank in maize crops was dominated by spring-germinating species, matching the sowing and emergence of each crop type.

5. Conclusions

Extensive farm management over the years (e.g., unfertilised and organic farming systems) was associated with higher species diversities but also higher seed abundance in the seedbank than conventional farming systems. From a function perspective, our results suggest that organic systems are the most suitable farming system for the maintenance of arable weed seedbanks. Given its positive effect, organic farming could potentially also benefit ecosystem functions and services. However, management to guarantee the maintenance of established weed abundances within appropriate thresholds that avoid affecting crop production is necessary.

Species assemblies and functional composition of the seedbank also depended on different farming systems. Long-term fertilised farming systems (both organic and conventional) filtered the arable seedbank community with traits indicative of fast life strategies and better competitive abilities, which might represent potential competitive communities to the crop when established.

Although the seedbank acts as a buffer of long-term management and crop sequence, the last crop sown significantly shaped the composition of the soil seedbank in the DOK trial. Thus, the specific management conducted in a given year should be carefully planned to shape the pool of seeds shed from the arable community to the soil.

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Spanish Ministry of Science, Innovation and Universities, the State Research Agency and the European Fund for Regional Development.

Author contributions

PM and JM designed and managed the DOK long-term trial. FXS designed the study and collected the soil samples; RRR and FXS conducted the seedling sampling. RRR analysed the data. RRR and FXS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data supporting the results will be archived in a public repository accessible at http://hdl.handle.net/2445/154837.

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Supporting information

Supplementary data associated with this article can be found in the online version of this article:

Appendix S1: Supplementary tables.

Table 1: Functional traits and levels or values considered in the functional diversity analyses with indication of the potential agro-ecosystem services (or disservices). "Prop" indicates proportion.

		Potential services	
Plant trait	**Trait levels**	**Response trait**	**Effect trait**
Raunkiær life form	Therophyte Hemicryptophyte Geophyte Chamaephyte	Potential to adapt to disturbance regimes	Potential to interfere with crop (potential disservice)
Growth form	Rosette Ascending or creeping Graminoid	Potential to capture environmental resources (light, space)	Potential to interfere with crop (potential disservice)
Soil seedbank longevity	Long-term (> 5 years) (prop reported) Short-term (1 - 5 years) (prop reported) Transcient (< 1 year) (prop reported)	Potential to endure in an ecosystem	Potential to interfere with crop in a long-term perspective (potential disservice)
Specific leaf area (SLA) (mm^2 mg^{-1})	Mean value	Potential to use radiation efficiently and compete for light	Potential to interfere with crop (potential disservice)
Plant height (cm)	Mean of maximum values at maturity reported	Potential to react to environmental and management conditions	Potential to compete with crop (potential disservice)
Seed weight (mg)	Mean value	Potential to react to environmental and management conditions	Potential to compete with crop (potential disservice)
Affinity to soil nutrient conditions	1 to 10 being 1 oligotrophic and 10 in nutrient rich soils	Potential to adapt to nutrient soil conditions	Potential to compete with crop under a given set of conditions (potential disservice)
Seasonality of germination	Autumn (prop) Spring (prop) Summer (prop) Winter (prop)	Breath of species adaptation	Potential to interfere with crop (potential disservice)

Table 2: Coefficients and their standard errors of the linear mixed-effect models testing the effects of the long-term farming systems and the current crop (i.e. maize or wheat) on the seedling density, species richness, Shannon's diversity index, Pielou's evenness index, on the functional richness, functional evenness, functional dispersion and functional redundancy of the soil seedbank. Orthogonal contrasts to compare the different levels of farming systems: conventional (CONFYM), mineral (CONMIN), organic (BIOORG), biodynamic (BIODYN) and unfertilized (NOFERT). Groups of farming systems were: fertilized systems (**Fert** = CONFYM, CONMIN, BIOORG and BIODYN), organic systems (**Org** as BIOORG and BIODYN) and conventional systems (**Con** as CONFYM and CONMIN). Statistical significance is indicated as · when P < 0.1; * when P < 0.05; **, P < 0.01; and ***, P < 0.001.

Contrasts	**Seed density** Estimate ± SE		**Species richness** Estimate ± SE		**Shannon** Estimate ± SE		**Evenness** Estimate ± SE	
Intercept	9.610 ± 0.112	***	2.467 ± 0.031	***	2.368 ± 0.079	***	0.695 ± 0.022	***
NOFERT vs. Fert	0.276 ± 0.038	***	0.057 ± 0.011	***	-0.066 ± 0.037	·	-0.034 ± 0.010	**
Org vs. Con	0.444 ± 0.086	***	0.226 ± 0.024	***	0.246 ± 0.083	**	-0.004 ± 0.023	
BIODYN vs. BIOORG	-0.283 ± 0.122	*	-0.057 ± 0.034		0.051 ± 0.117		0.033 ± 0.032	
CONFYM vs. CONMIN	-0.143 ± 0.122		-0.047 ± 0.034		-0.022 ± 0.117		0.010 ± 0.032	
WHEAT vs. MAIZE	-0.158 ± 0.109		0.012 ± 0.030		0.207 ± 0.105	·	0.060 ± 0.029	*
<u>Interactions</u>								
NOFERT vs. Fert × WHEAT vs. MAIZE	0.127 ± 0.054	*	0.013 ± 0.015		-0.102 ± 0.052	·	-0.032 ± 0.014	*
Org vs. Con × WHEAT vs. MAIZE	-0.060 ± 0.122		-0.026 ± 0.034		0.048 ± 0.117		0.014 ± 0.032	
BIODYN vs. BIOORG × WHEAT vs. MAIZE	0.197 ± 0.172		0.060 ± 0.048		-0.087 ± 0.165		-0.045 ± 0.045	
CONFYM vs. CONMIN × WHEAT vs. MAIZE	-0.006 ± 0.172		-0.009 ± 0.048		-0.023 ± 0.165		0.000 ± 0.045	

Contrasts	**Functional richness**		**Functional evenness**		**Functional dispersion**		**Functional redundancy**	
Intercept	0.073 ± 0.003	***	0.678 ± 0.011	***	0.204 ± 0.005	***	0.304 ± 0.010	***
NOFERT vs. Fert	0.004 ± 0.001	***	0.008 ± 0.005	·	-0.006 ± 0.003	*	-0.008 ± 0.005	

Org vs. Con	0.011 ± 0.003	***	-0.010 ± 0.010		-0.004 ± 0.006		0.023 ± 0.011	*
BIODYN vs. BIOORG	-0.001 ± 0.004		0.019 ± 0.015		-0.001 ± 0.008		0.014 ± 0.015	
CONFYM vs. CONMIN	-0.005 ± 0.004		0.015 ± 0.015		-0.002 ± 0.008		-0.002 ± 0.015	
WHEAT vs. MAIZE	-0.009 ± 0.003	**	0.018 ± 0.011	·	-0.010 ± 0.007		0.035 ± 0.014	*
Interactions								
NOFERT vs. Fert × WHEAT vs. MAIZE	0.003 ± 0.002		-0.007 ± 0.005		-0.004 ± 0.004		-0.017 ± 0.007	*
Org vs. Con × WHEAT vs. MAIZE	0.000 ± 0.004		-0.007 ± 0.012		0.001 ± 0.008		0.005 ± 0.015	
BIODYN vs. BIOORG × WHEAT vs. MAIZE	0.000 ± 0.005		-0.015 ± 0.017		0.002 ± 0.012		-0.025 ± 0.022	
CONFYM vs. CONMIN × WHEAT vs. MAIZE	0.002 ± 0.005		-0.003 ± 0.017		0.000 ± 0.012		0.001 ± 0.022	

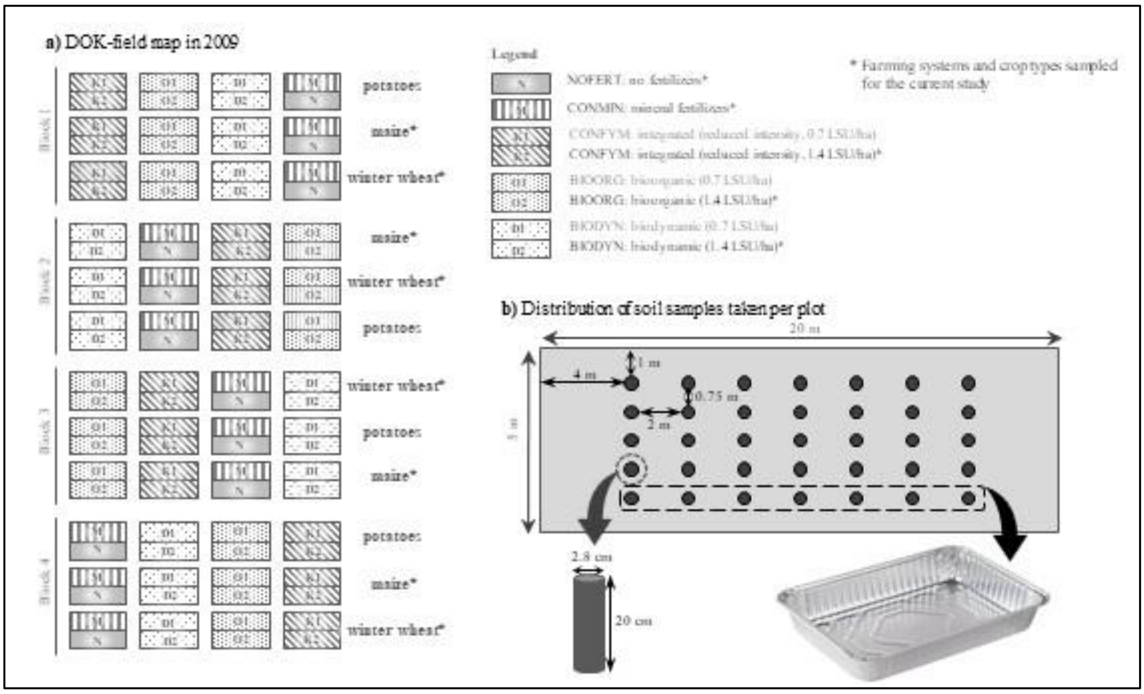

Figure 1: a) DOK trial field map and crops sown in the year of sampling (2009). * indicate crop types and farming systems sampled for the current study. b) Distribution of soil samples taken per plot, sizes of soil cores sampled and distribution of cores gathered in each tray (obtaining a total of 5 trays per plot).

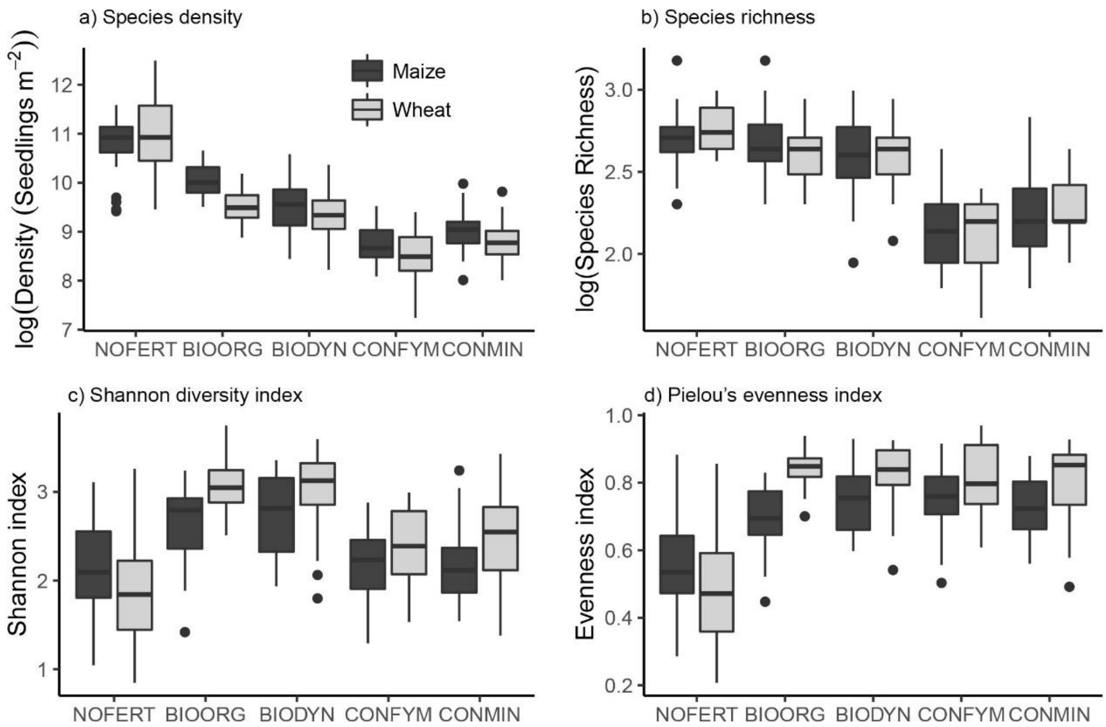

Figure 2: Boxplots of a) seedling density, b) species richness, c) Shannon diversity index and d) Pielou’s evenness index of unfertilised (NOFERT), organic (BIOORG), biodynamic (BIODYN), conventional (CONFYM) and mineral (CONMIN) farming systems of the DOK trial of both maize and wheat crops, based on the 20 soil seedbank samples per farming system and crop type.

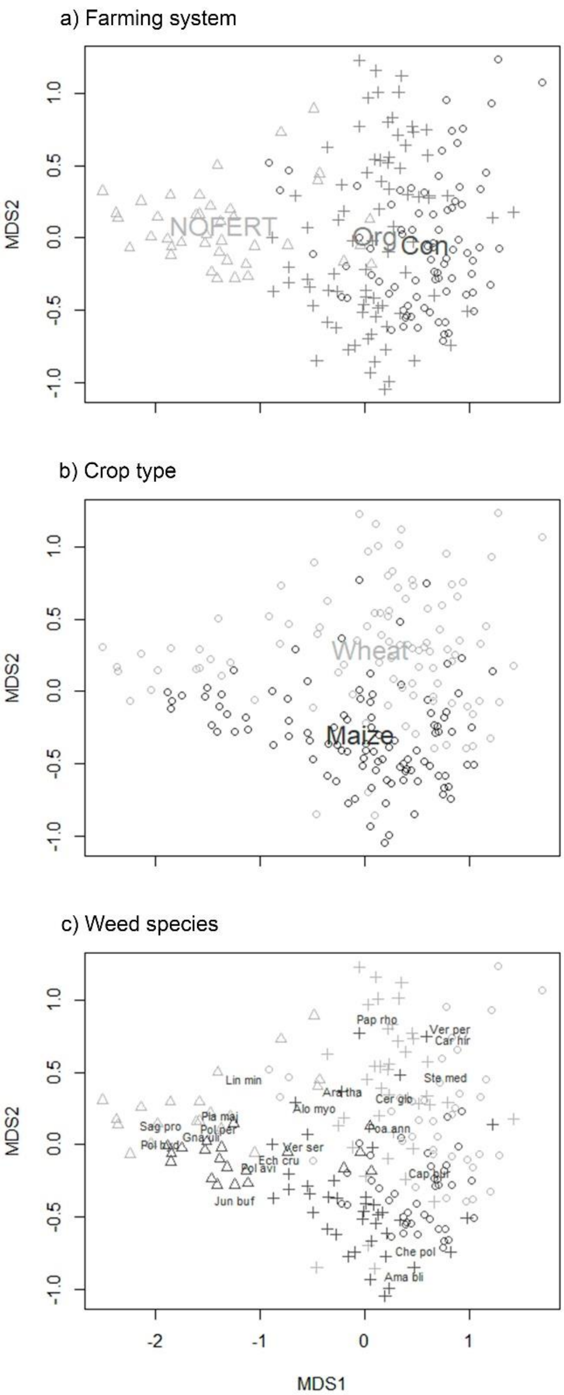

Figure 3: Site ordination (NMDS) based on floristic similarities between conventional (CONFYM and CONMIN, circles), organic/biodynamic (BIOORG and BIODYN, crosses) and unfertilised (NOFERT, triangles) farming systems (DOK trial) of both maize (dark grey) and wheat (light grey) crops of 200 soil seedbank samples (k = 2, r^2 nonmetric fit = 0.973). a) Farming system types fitted onto the ordination (r^2 = 0.273, P < 0.001); b) Crop type sown in the last season fitted onto the ordination (r^2 = 0.062, P < 0.001). c) Labels of most present

species fitted onto the ordination: Alo myo: *Alopecurus myosuroides*; Ama bli: *Amaranthus blitoides*; Ara tha: *Arabidopsis thaliana*; Cap bur: *Capsella bursa-pastoris*; Car hir: *Cardamine hirsuta*; Cer glo: *Cerastium glomeratum*; Che pol: *Chenopodium polyspermum*; Ech cru: *Echinochloa crus-galli*; Gna uli: *Gnaphalium uliginosum*; Jun buf: *Juncus bufonius*; Lin min: *Chaenorhinum minus*; Pap rho: *Papaver rhoeas*; Pla maj: *Plantago major*; Poa ann: *Poa annua*; Pol avi: *Polygonum aviculare*; Pol hyd: *Polygonum hydropiper*; Pol per: *Polygonum persicaria*; Sag pro: *Sagina procumbens*; Ste med: *Stellaria media*; Ver per: *Veronica persica*; Ver ser: *Veronica serpyllifolia*.

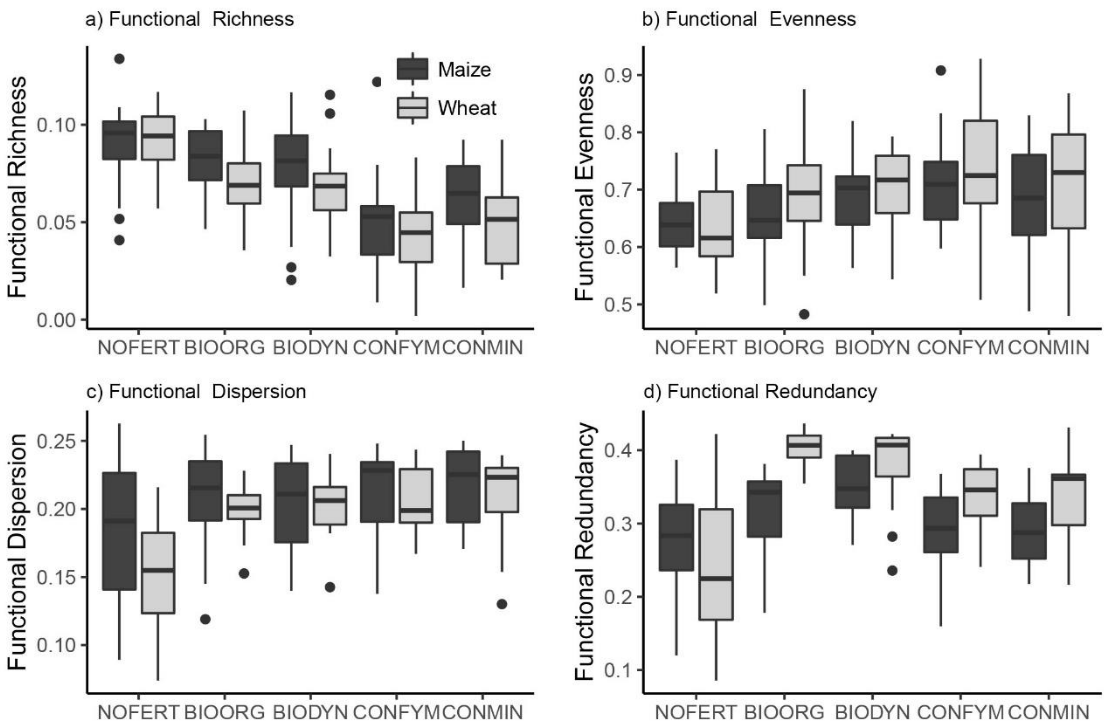

Figure 4: Boxplots of a) functional richness, b) functional evenness, c) functional divergence (FDis index) and d) functional redundancy of unfertilised (NOFERT), organic (BIOORG), biodynamic (BIODYN), conventional (CONFYM) and mineral (CONMIN) farming systems of the DOK trial of both maize and wheat crops, based on the 20 soil seedbank samples per farming system and crop type. The functional traits considered for the calculation of functional diversity indices were: the Raunkiær life form, growth form, soil seedbank longevity, SLA, plant height, seed weight, affinity to soil nutrient conditions and season of germination.

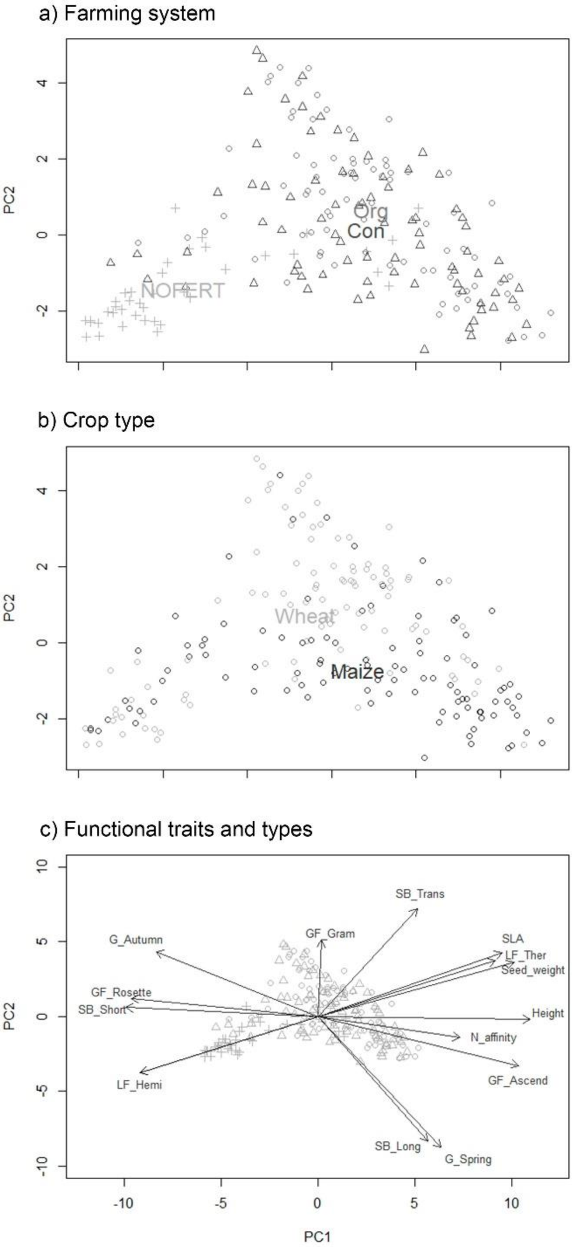

Figure 5: Ordination diagrams of the first two PCA axes based on the functional composition (Community Weighted Mean, CWM) of 200 seedbank samples from: conventional (CONFYM and CONMIN, circles), organic/biodynamic (BIOORG and BIODYN, crosses) and unfertilised (NOFERT, triangles) farming systems (DOK trial) of maize (dark grey) and wheat (light grey) crops. Farming system (a) and crop type (b) labels are placed on the average values obtained on the first two PCA axis. c) Direction of the most significant response factors of functional traits considered for the CWM index: "LF_Thero": life form therophyte; "LF_Hemi": life form hemicryptophyte; "GF_Rosette": growth form rosette; "GF_Ascend": growth form ascending or

creeping; “GF_Gram”: growth form graminoid; “SB_Long”: long-term seedbank; “SB_Short”: short-term seedbank; “SB_Trans”: transcient seedbank; “SLA”: specific leaf area; “Height”: plant canopy height; “Seed_Weight”: seed weight; “N_affinity”: nutrient affinity; “G_autumn”: autumn germinating species; and “G_Spring”: spring germinating species.