



Crop genetic diversity benefits farmland biodiversity in cultivated fields



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ABSTRACT

This study tested whether increasing crop genetic diversity benefited farmland biodiversity in bread wheat (*Triticum aestivum*) fields, using an experimental approach in which arthropod and wild plant diversity were compared in a genetically homogeneous wheat variety vs. a variety mixture. The diversity of wild plant species was not affected by crop genetic diversity. However, we showed for the first time a positive impact of crop genetic diversity on below (collembola) and aboveground arthropod (spiders and predatory carabids) diversity at field scale in agroecosystems, which may be caused by a wider variety of food resources or more complex crop architecture. Increasing crop genetic diversity could therefore be an easy-to-implement scheme benefiting farmland biodiversity.

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1. Introduction

Crop genetic diversity has been decreasing steadily in the agricultural landscapes of developed countries since the early 20th century (FAO, 1997; Secretariat of the Convention on Biological Diversity, 2006). This is mostly due to the widespread replacement of genetically diverse traditional varieties or landraces by homogeneous modern varieties (Hoisington et al., 1999), leading to decreased genetic diversity in the fields, both within and between varieties. Hence, in spite of an increasing number of registered crop varieties since the sixties, the majority of agricultural land in developed countries is now covered with a few “winning” productive varieties, with generally a single crop per field, so that the actual cultivated diversity is in fact low (e.g. FranceAgriMer and ARVALIS Institut du Végétal, 2009 in France). The resulting crop

genetic homogenization is postulated to threaten the sustainability of production systems, and several studies now emphasize the importance of both inter- (e.g. Altieri, 1999; Lin, 2011) and intra-specific (e.g. Hajjar et al., 2008; Macfadyen and Bohan, 2010) crop diversity to increase and stabilize crop yield, via e.g. improved pest control (see e.g. Tooker and Frank, 2012 for a review).

Another potential consequence of decreased crop genetic diversity that has received little attention so far is erosion of wild biodiversity in agroecosystems. Previous studies in natural systems (e.g. Whitham et al., 2006) have shown that the phenotype (hence the genotype) of some plant species may affect the composition of the dependent community. These particular species, referred to as foundation species, are abundant in the ecosystem (often, but not always, tree species, Whitham et al., 2006). Because they represent a large fraction of the biomass of an ecosystem, they structure a community by creating locally stable conditions for other species (e.g. habitats and food sources) and by modulating and stabilizing fundamental ecosystem processes (see Ellison et al., 2005 for definitions). The impact of the genotype of a single species on a community is known as a “community phenotype”, i.e. an effect of genes at the community level (“Community genetics”, Whitham et al., 2003). High genetic and phenotypic diversity in foundation

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species can result in a diversity of local environments, thereby benefiting species diversity in the dependent community and affecting ecosystem processes (Bangert et al., 2005; Whitham et al., 2006; Wimp et al., 2004). Although well documented in natural ecosystems, the influence of genetic diversity on community diversity has never been investigated in agroecosystems. Several lines of evidence nonetheless suggest that crop genetic diversity can greatly affect wild species diversity. First, crops are dominant in terms of biomass in a field and can be considered foundation species. Second, crops are known to be involved in numerous (though altered, Macfadyen and Bohan, 2010) interactions with non-crop species, which may create community phenotypes similar to wild foundation species. These interactions include exploitation and interference competition with weed species (e.g. allelopathy, demonstrated for several cereals: Belz, 2007; Bertholdsson, 2010), trophic interactions with phytophages (e.g. species that feed on root and leaf secretions or excreta), or mutualistic interactions via the creation of microhabitats for predators by below and aboveground vegetative architecture (e.g. Johnson, 2008). As a result, decreased crop genetic diversity should alter farmland biodiversity within and among fields, via a reduction in the diversity of available ecological niches or food sources (Bangert et al., 2005).

The present study assessed the relationship between in-field crop genetic diversity and the species diversity of several taxonomic groups (springtails, ground-dwelling macroarthropods and plants), using an experimental approach in the field. We worked with winter wheat (*Triticum aestivum*), the main crop in the study region, which also exhibits large phenotypic variation among varieties. Species diversity was compared between plots sown with a pure line variety and plots sown with a combination of several varieties. The following predictions were tested: (1) local (α) diversity at each sampling point should be higher in the variety mixture than in the pure line variety, due to the diversity of genotypes (and therefore phenotypes) surrounding each sampling point; (2) β -diversity (between sampling points) should be low within the pure variety because one wheat genotype should be preferentially associated with one community phenotype, whereas β -diversity in the variety mixture should be higher due to high spatial heterogeneity of wheat genotype associations in the field; (3) consequently, γ -diversity, the sum of α - and β -diversity, should be higher in the variety mixture than the pure line variety. We discuss the most likely underlying mechanisms, as well as possible consequences for ecosystem services and opportunities for agricultural sustainability.

2. Methods

The experiment took place in an organic farm in northern France. In winter 2007–2008 ten contiguous square plots (60 m wide) were sown with either a “pure line” bread wheat variety (*T. aestivum* “Renan”, INRA, five plots) or a genetically diverse seed mixture including 30 landraces and several pure line varieties, among which the “Renan” variety. Pure line varieties are obtained by successive (usually 6–10) self-fertilizations of a few selected plants so that all plants are eventually highly homozygous and genetically identical. These two crop diversity treatments were distributed in a checkerboard-like pattern (see Appendix A). This limited confounding spatial effects but did not fully discard them, owing to the partly unbalanced experimental design that was constrained by field shape. However, these confounding effects appeared to be minor: for example, the only plot not bordered by the surrounding matrix (plot R2, Appendix A) did not exhibit extreme ecological diversities compared to other plots in the same treatment. No mechanical or chemical treatment was applied between sowing and harvest, as is often the case in organic farming; plots

were surrounded by a wheat variety not used in the experiment itself.

2.1. Community sampling

Springtails (collembola) were sampled at the beginning of May 2008, using five soil cores (5 cm diameter, 12 cm deep) per plot (one in the center of the plot, the other four at the center of each quarter). After ten days of extraction with the Berlese method (Edwards and Fletcher, 1971), individuals were counted and identified to species level. Water content (dry weight/wet weight) and pH (method NF ISO 10390) were also measured in each soil core.

Ground-dwelling macroarthropods were sampled twice in May and June 2008, during two-week trapping sessions separated by a two-week interruption. To this end, five pitfall traps (9.5 cm diameter, 11.4 cm deep, filled with ethylene glycol) were located at the corners and center of a 10 m \times 10 m square centered in each plot. This distribution reduced the capture of individuals from neighboring plots, while maintaining enough distance between the five pitfall traps of a same plot to consider them as relatively independent replicates. The two most abundant groups, carabids and spiders, were identified to species level. All individuals of small carabid species (≤ 4 mm) without identification were grouped (190 individuals, 6.8% of total carabids) and six larger individuals could be identified to genus level only. All spider juveniles that could not be identified to species level were discarded (1674 individuals, 20% of total spiders); the number of discarded individuals was however not significantly different across crop diversity treatments ($F_{1,8} = 4.41$, $P = 0.07$). For aboveground and belowground invertebrates, other taxonomic groups were observed in the samples (including flies, ants, non-carabid Coleoptera and slugs above ground; mites and earthworms below ground), but these represented a small fraction of total abundance (1–5%) and a small number of species.

Finally, all wild plants growing in the experimental area were sampled twice, at the beginning of May and June 2008. At each sampling date, all plant species were recorded in 25 1 m² quadrats evenly distributed within each plot, i.e. a total of 500 quadrats. All individual plants were identified to species level. The quadrats were divided into 25 20 cm \times 20 cm squares to estimate abundance as the number of squares where a species was present.

2.2. Wheat individual measurements

Morphological and phenological characters that are classically used to describe phenotypes in wheat (e.g. IBPGR Secretariat, 1985; Murphy et al., 2008; UPOV, 1996) were measured to assess wheat phenotypic diversity within each crop diversity treatment: tiller number (five quadrats per plot, 1068 individuals), flowering date (eight quadrats per plot, 2205 individuals), total height at maturity, length, width and position along the stalk of the first leaf, and spike number (four samples of ten individuals per plot). Although these traits were not chosen on the basis of involvement in interspecific interactions, but to provide a general index of phenotypic diversity, some are nonetheless known to influence plant–plant interactions (e.g. plant height and competition for light) or plant–invertebrate interactions (e.g. plant architecture creating microhabitats, Langellotto and Denno, 2004).

For each measured character, we checked that wheat diversity was actually different between the two crop diversity treatments with a non-parametric Fligner test for homogeneity of variance. Wheat phenotypic diversity was then summarized within each plot by normalizing and combining the five morphological characters describing vegetation structure (total height, length, width and position of the first leaf, spike number) to calculate Rao's diversity coefficient (Rao, 1982) with the Mahalanobis distance,

which removes correlations between morphometric characters measured on the same individual. A permutational test of homogeneity of multivariate dispersion (R, library *vegan*; Anderson, 2006; Anderson et al., 2006) was used to verify that the diversity measured over these five characters was highest in the variety mixture.

Finally wheat density (number of individuals per unit area) was measured in each plot (six quadrats per plot) and we checked that there was no difference in wheat density between crop diversity treatments using a linear model with observer and treatment as fixed variables, and plot as a random variable.

2.3. Statistical analyses

For all analyses below, spiders from the family Linyphiidae were analyzed separately to account for differences in the field colonization dynamics between these small late-colonizing, ballooning spiders and spiders from other families. For carabids, all analyses were performed on the full dataset and on predatory and herbivorous species separately.

Linear models were analyzed with SAS software (version 9.1, SAS Institute Inc. 2006, Cary; proc GLM and MIXED) and multivariate analyses as well as resampling procedures with R software (version 2.10.1, R Development Core Team, 2009, Vienna; library *vegan*).

Local community diversity (α -diversity within sampling units: quadrats, soil cores or pitfall traps) was measured using species richness and Shannon Diversity Index. We first tested the effect of wheat diversity treatment on these two dependent variables using linear mixed effects models with the following core structure: crop diversity treatment (pure line variety vs. variety mixture), sampling session and their interaction (dropped if non-significant) were included as fixed effects, and 60 m \times 60 m plot as a random effect, to account for the spatial clustering of data (replicates clustered within plots). This general model was used a couple of times and is subsequently referred to as “Model 1”. A number of fixed covariates were added to this core structure depending on the taxonomic group but discarded if non-significant: soil pH and water content for springtails (not retained in the final model: $P > 0.60$ for both, and not influenced by the crop diversity treatment: $P > 0.10$), distance to field edges for ground-dwelling arthropods to account for spring recolonization (not retained), and spatial coordinates for all taxa to account for spatial autocorrelation of data (not retained for springtails only).

Second, the relationship between species diversity (richness or Shannon Index) and wheat phenotypic diversity was examined to get a more quantitative picture of the effect of wheat diversity on communities. This was done for each above-ground taxon using linear mixed effects models in which community diversity (richness or Shannon) was explained by Rao's coefficient of phenotypic diversity (calculated on wheat aerial architecture) and sampling session (fixed effects); plot was included as a random effect.

2.3.1. Local community diversity

We first checked that observed differences in the number of individuals were not a mere by-product of differences in wheat productivity (“more individuals hypothesis”, Srivastava and Lawton, 1998): a greater biomass offers more resources, hence potentially more individuals. The relationship between number of individuals and wheat biomass was tested with a linear mixed effects model where abundance was a function of either of two proxies for wheat biomass (mean crop height per plot or mean individual spike number per plot) and session (fixed effects), as well as plot (random effect). This was done for all taxa except springtails, which were sampled too early for wheat phenotypic measures to be meaningful. We also tested whether the abundance of taxonomic groups

differed between wheat diversity treatments using Model 1 with total abundance as a dependent variable.

Finally, for all taxa with a significant or marginally significant effect of wheat genetic diversity on species richness or Shannon Index, permutation analyses were performed to separate the effects of abundance vs. diversity. From the original dataset, 1000 rearranged datasets were produced by randomly reallocating each sampled individual to one local community (sampling unit), while keeping the sample size (number of individuals, i.e. abundance) of sampling units constant. Each rearranged dataset was analyzed using Model 1. We then compared the observed F -value for crop diversity treatment (pure line vs. variety mixture) obtained from the original dataset to the distribution of F -values from permuted communities (see Appendix C). When the F -value for the original dataset fell outside of the 95% percentile, the effect of crop diversity on richness or Shannon Index was not explained by differences in abundance.

2.3.2. Community similarity

In addition to local biodiversity indices, we examined whether community composition differed between crop diversity treatments. We specifically tested whether individual samples (pitfall traps, soil cores or plant quadrats) were more similar to each other within the pure line treatment than within the variety mixture, using the non-Euclidean Bray–Curtis distance to measure dissimilarity. The significance of the difference in local community dissimilarities between the pure line variety and the variety mixture was then tested with a permutational test of homogeneity of multivariate dispersion (Anderson, 2006 and R library *vegan*), which permutes model residuals to generate a permutation distribution of F under the Null hypothesis of no difference in dispersion between groups.

2.3.3. Total species richness

To test for differences in total richness independently of differences in abundance, we used the resampled communities and we compared the mean γ -diversity in these communities to the observed species richness within each crop diversity treatment using one-tail t -tests. The observed richness was expected to be higher (respectively lower) than the resampled richness in the variety mixture (respectively in the pure line variety).

3. Results

Whereas there was no difference in wheat density between crop diversity treatments ($F_{1,8} = 0.00$, $P = 0.97$), the two wheat diversity treatments exhibited contrasting levels of phenotypic diversity: for almost all morphological and phenological measures, individual variance and multivariate dispersion were higher in the variety mixture than in the pure line variety (see Appendix B). There was also a significant difference in biomass between the two crop diversity treatments, with taller (111 ± 23 cm vs. 66 ± 6 cm, $P < 0.001$) and more ramified (4.5 ± 2.4 vs. 3.7 ± 2.0 tillers, $P = 0.02$) plants in the variety mixture than in the pure line variety.

A total of 48 plant species, 1057 springtail individuals from 19 species, 2781 carabid individuals from 20 species and one group of very small carabids, and 6625 spider individuals from 48 species (linyphiids: 4723 individuals, 15 species; other spiders: 1902 individuals, 33 species) were sampled.

3.1. Local community diversity

There was a significant effect of wheat diversity treatment on α -diversity (Fig. 1), with higher diversity in the variety mixture for springtails (species richness only, $F_{1,8} = 5.38$, $P = 0.049$),

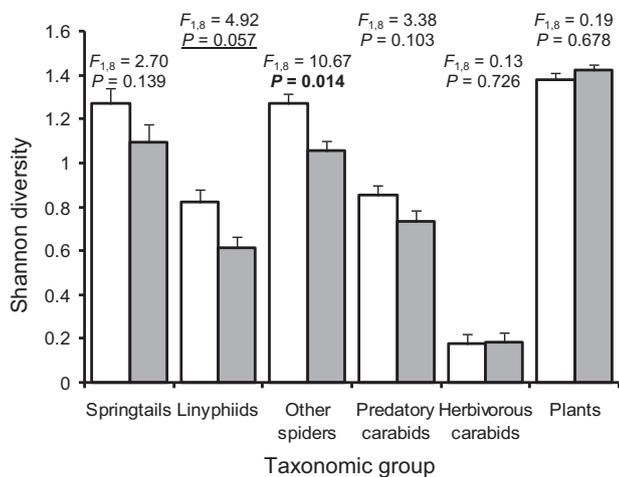


Fig. 1. Shannon Diversity Index for all studied taxonomic groups in the variety mixture (white bars) and in the pure line variety (gray bars). Error bars represent standard errors. F - and P -values for the crop diversity treatment effect in the ANOVA are given.

linyphiids (species richness only, $F_{1,8} = 7.48$, $P = 0.026$; marginal significance for Shannon Index) and other spiders (Shannon Index only); regardless of statistical significance, diversity was always higher in the variety mixture than in the pure line variety in these taxa. In contrast, plants and carabids were not influenced by wheat diversity ($P > 0.10$), regardless of trophic level for the latter (no difference between predators and herbivores). Community diversity was in general higher during the second sampling session for both crop diversity treatments (non-significant interaction between wheat diversity treatment and session). When the effect of wheat diversity was examined more quantitatively, via a correlation with Rao's diversity coefficient, there were significant positive effects of phenotypic diversity on linyphiid species Shannon Index ($F_{1,8} = 7.85$, $P = 0.023$) and predatory carabid species richness ($F_{1,8} = 5.37$, $P = 0.049$). No effect was found for the other taxa ($P > 0.10$).

No effect of wheat biomass ($P > 0.10$) was found on total abundance for all taxa except linyphiids, whose abundance was positively affected by mean crop height ($F_{1,8} = 9.44$, $P = 0.015$). In fact, only linyphiid abundance was positively affected by wheat genetic diversity ($F_{1,8} = 10.52$, $P = 0.012$). For all other taxa, there was no difference in abundance between the variety mixture and the pure line variety ($P > 0.60$). When the effect of abundance was removed by comparing observed communities to randomly assembled communities with the same local abundances, the positive effect of wheat diversity on springtail species richness and spider (other than linyphiids) Shannon Index remained (springtail richness: observed F : 5.38, simulated F (quantile 95%): 3.33; other spider Shannon Index: observed F : 10.67, simulated F : 4.11). In contrast, the F -values of the ANOVAs on linyphiid species richness and Shannon Index in observed communities were not different from random communities (observed F : 7.48, simulated F : 11.69 and observed F : 4.92, simulated F : 4.93 respectively), suggesting that the positive effect of wheat diversity on linyphiids resulted from an increase in local abundance and not diversity per se.

3.2. Community similarity

The homogeneity of multivariate community dispersion between the pure line variety and the variety mixture was tested for each taxon: for non-linyphiid spiders, community dispersion across sites was higher in the variety mixture compared to the pure line variety ($P = 0.004$, average distance to spatial median in the variety

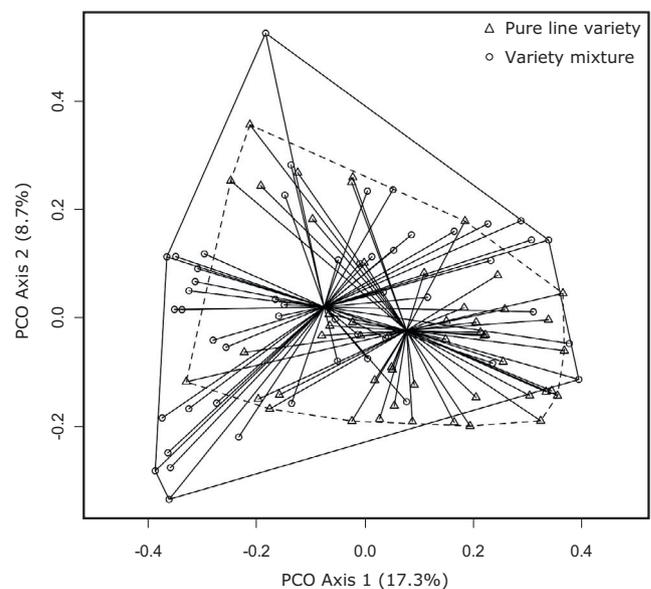


Fig. 2. Principal coordinate ordination of the non-linyphiid spider data, showing assemblages from the variety mixture (circles, solid line) and the pure line variety (triangles, dashed line).

mixture: 0.37; in the pure line variety: 0.30; Fig. 2), indicating that local communities were more similar to one another in the pure line variety. For plants there was a significant but small difference ($P = 0.036$, average distance to spatial median in the variety mixture: 0.45; in the pure line variety: 0.47) with a higher dispersion in the pure line variety, but this effect was mainly caused by strong spatial autocorrelation and inter-plot differences in species composition. For other taxa (springtails, linyphiids and carabids), there was no difference in dispersion between the two crop diversity treatments ($P > 0.10$).

3.3. Total species richness

When γ -diversity in the variety mixture and the pure line variety were compared to γ -diversity in randomly permuted communities, total species richness in the pure line variety was lower than expected for all taxa ($P < 0.0001$, Table 1) whereas total species richness in the variety mixture was almost always higher than expected ($P < 0.0001$ except for predatory carabids and plants). For plants, observed species richness was significantly lower than expected in both crop diversity treatments, reflecting local specific spatial aggregation as commonly observed for weed species (Rew and Cousens, 2001).

4. Discussion

Overall, there was a general positive correlation between wheat diversity and all levels of species diversity (α , β , γ) that was consistent across most studied arthropod taxa. Although the intensity and significance of the effect varied, species richness and/or species diversity of arthropod communities were consistently higher in the variety mixture than in the pure line variety. Plants were the only group to exhibit no difference between the two wheat diversity treatments. This result was however not surprising because most plants were typical annual weed species; the latter generally exhibit patchy distributions caused by environmental heterogeneities or demographic factors (e.g. limited dispersal, Rew and Cousens, 2001). Hence, in comparison to studies that demonstrated an impact of genetic diversity on plant community structure or invasibility (e.g. Booth and Grime, 2003; Crutsinger et al., 2008;

Table 1
Comparison of species richness in the variety mixture vs. the pure line variety in each taxon or trophic group.

Taxa or trophic groups	Number of shared species	Number of species unique to		Total number of species		Mean number of species after randomization ^a	
		Mixture	Pure line	Mixture	Pure line	Mixture	Pure line
Springtails	15	4	0	19	15	16.6 <i>P</i> <0.001	17.2 <i>P</i> <0.001
Linyphiids	10	4	1	14	11	13.5 <i>P</i> <0.001	12.5 <i>P</i> <0.001
Other spiders	16	11	6	27	22	24.8 <i>P</i> <0.001	25.8 <i>P</i> <0.001
Carabids	12	6	3	18	15	16.6 <i>P</i> <0.001	16.8 <i>P</i> <0.001
Predators	7	2	1	9	8	8.9 <i>P</i> =0.22	9.0 <i>P</i> <0.001
Herbivores	3	4	1	7	4	5.8 <i>P</i> <0.001	5.2 <i>P</i> <0.001
Plants	33	8	7	41	40	43.4 <i>P</i> =1	43.5 <i>P</i> <0.001

^a The total number of species in each crop diversity treatment is compared to the mean number of species observed in 1000 randomized datasets (see text for details). *P*-values of one-tail *t*-tests indicate whether the observed number of species in the variety mixture (respectively in the pure line variety) is significantly higher (respectively smaller) than expected at random.

Fridley and Grime, 2010), the short time span of the experiment (six months between wheat sowing and the last plant survey) was probably not sufficient for a spatial reorganization of plant communities via seed dispersal and differential growth. In addition, environmental variation is likely to have a much stronger impact than genetic diversity on competition among plant species (Johnson et al., 2008) and theory predicts variable effects of the genetic diversity of a foundation species on the diversity of subordinate species, depending on environmental heterogeneity (Gibson et al., 2012). This homogeneity of weed communities between the two crop genetic diversity treatments also suggests that the observed differences in arthropod diversity were mostly attributable to differences in wheat, not weeds.

Our results represent the first experimental evidence that crop genetic diversity can benefit farmland biodiversity in agroecosystems, and one of the rare examples where the effects of the genetic diversity of a foundation species are observed at a relatively large scale under realistic environmental conditions (but see references on *Populus* species, e.g. Wimp et al., 2004; and a number of field studies examining the impact of crop genetic diversity on herbivore abundance, not diversity, e.g. Hambäck et al., 2010; reviewed in Tooker and Frank, 2012). The higher local diversity in the variety mixture for most arthropod groups (springtails, spiders, and, to a lesser extent, predatory carabids) is however consistent with comparable small-scale experimental studies on non-crop herbaceous species (Crutsinger et al., 2006; Johnson et al., 2006; Jones et al., 2011) and may involve similar mechanisms. First, differences in diversity may arise as a direct consequence of differences in abundance (“more individuals hypothesis”, Srivastava and Lawton, 1998) caused by differences in biomass between diversity treatments (e.g. higher aboveground net primary productivity with higher genotypic diversity of *Solidago altissima* cultures in Crutsinger et al.’s experiment, 2006). Here, this explanation could be rejected for most taxonomic groups: the observed differences in diversity were generally independent of arthropod abundance and wheat productivity, showing that resource quality and not quantity caused higher biodiversity. For linyphiids, however, the higher species richness and Shannon Index in the variety mixture vs. the pure line variety were mainly mediated by an increase in the number of individuals, partly (but not only) due to higher wheat biomass. Hence for this group the relative roles of wheat biomass vs. genetic diversity per se cannot be differentiated. Although it is likely that differences in biomass are the key factor that controls linyphiid species richness by affecting the number of individuals, we cannot

exclude that crop genetic diversity also increases productivity of in-field communities via a more efficient use of resources (including web-fixing sites), with consequences on community diversity (Crutsinger et al., 2006; Genung et al., 2010).

In the cases where differences in species diversity were not controlled by the number of individual arthropods, at least two alternative mechanisms may explain higher species diversity in the mixture of wheat varieties. First, the taxonomic diversity hypothesis states that higher genetic diversity of the foundation species increases the diversity of resources available to herbivores (e.g. Bukovinszky et al., 2008 in *Brassica* lines; or Crutsinger et al., 2006 in *S. altissima* plots). This mechanism may apply to springtails, which may be offered a wider variety or more accessible food resources in the variety mixture, directly through biochemical variation in root systems or indirectly through associated microflora. The taxonomic diversity hypothesis is however a much less likely explanation for differences in aboveground communities, where the only herbivore group (carabids) was unaffected by wheat genetic diversity. Instead, the structural heterogeneity hypothesis states that higher genetic diversity of the foundation species generates more complex vegetation architecture (Brose, 2003; Harvey et al., 2008). Several studies have shown that ground-dwelling arthropods, especially spiders, were sensitive to vegetation structural diversity (Brose, 2003; Hansen, 2000; Jeanneret et al., 2003; Langellotto and Denno, 2004) or that arthropod abundance and richness were higher on structurally complex plant genotypes (Johnson and Agrawal, 2005 in *Oenothera biennis*). Here we observed a significant effect of wheat morphological diversity on spiders and predatory (but not herbivorous) carabids, which provides support for a possible role of wheat architectural diversity in increasing species diversity, e.g. by creating multiple micro-habitats, although other mechanisms may be involved.

At the crop diversity treatment level, total (γ) species diversity was also higher in the variety mixture than in the pure line variety, which was much more due to the increase in local (α) species diversity than to among-sampling-unit differences in community composition (β -diversity): heterogeneity between communities was significantly higher in the variety mixture for non-linyphiid spiders only. This may be caused by the relatively large number of rare species found for all taxa except plants in the variety mixture vs. the pure line variety. These species represented 20–57% of species present in the mixture, but accounted for a small number of individuals, reflecting the strong dominance of one or a few species (e.g. *Pardosa agrestis* in spiders) and explaining the high similarity

between local communities. For non-lynyphiid spiders, this pattern of dominance was found in the pure line variety only, hence the difference in β -diversity.

4.1. Limitations and perspectives

One key limitation of our approach is that two crop diversity treatments only were compared (pure line variety vs. highly diverse mixture), with a single variety in the pure line variety treatment. As a result, we cannot make firm conclusions on the true role of genetic or phenotypic diversity per se vs. a variety effect on the diversity of farmland species. However, several facts and lines of evidence suggest that the difference in species diversity observed between the two treatments is caused by differences in genetic diversity. First, the pure line variety “Renan” was included in the variety mixture, although at a low frequency (<10%), so that a variety effect (repulsion of several species by the pure line variety) can be partly discarded. Second, and most important, wheat morphological diversity correlated positively with species diversity for two taxonomic groups, which cannot be explained by a mere variety effect. An additional limit of incomplete crop diversity treatments is that the actual effect of diversity vs. biomass on community diversity cannot be differentiated for the one taxonomic group (lynyphiid spiders) that exhibited differences in abundance between the two treatments. More generally, we cannot distinguish additive from interactive processes, i.e. processes resulting from the simple combination of community phenotypes in monocultures vs. processes that are non-predictable from isolated genotypes only, nor can we point out the exact source of wheat variability involved in community diversity (e.g. biochemical and/or architectural).

To confirm these results, the next essential step is therefore to consider a larger range of diversity levels and to compare several wheat varieties grown in monocultures vs. plots containing contrasting numbers of wheat varieties, as in similar studies exploring the relationship between a number of genotypes and the diversity of associated communities (Crutsinger et al., 2006; Johnson et al., 2006). Such full experimental design, ideally based on neighbor-balanced Latin square designs, is the only way to discriminate additive vs. interactive mechanisms for the effects of genetic diversity (Hughes et al., 2008; Loreau and Hector, 2001). Two genotypes can have very similar or very different phenotypic traits involved in interspecific interactions, so that the genetic variance for these traits can be same on average whether one compares two or many genotypes (Hughes et al., 2008). Hence, there is a need to go beyond the number of genotypes and to quantify phenotypic diversity, as was done in the present study. This quantification is necessary to confirm that genotypic diversity is associated with phenotypic diversity, and to elucidate the underlying genetic and ecological mechanisms.

Finally, future work should also investigate whether genetic diversity impacts farmland biodiversity for other crop species and other agricultural systems. The diversity and identity of plant and invertebrate communities in cultivated fields depend strongly on agricultural practices (e.g. conventional vs. organic farming, Bengtsson et al., 2005) and on crop type (Hawes et al., 2009; Macfadyen and Bohan, 2010; Smith et al., 2008). Hence, our results under organic farming may not apply to conventional farming, because most taxonomic groups (including plants and predatory insects) show decreased species richness under conventional farming (Bengtsson et al., 2005). In contrast, a positive effect of crop genetic diversity on species diversity has already been observed in a wide range of foundation species, from forbs to trees (Whitham et al., 2006), so that such effect is expected in other crop species. Note however that Hambäck et al. (2010) observed no effect of the genetic diversity of *Brassica oleracea* on the abundance of two herbivorous species. Considering a variety of crop species would

also broaden the range of phenotypic traits involved in interspecific interactions and may provide useful information to identify some of the mechanisms for the relationship between genetic and specific diversity.

4.2. Conservation benefits of crop genetic diversity

Genetically heterogeneous crops, which were (and still are) widely used in subsistence agriculture to secure yield (Smithson and Lenne, 1996), have received increasing attention recently, because this practice is believed to improve the sustainability of agriculture. The current genetic homogenization of crops likely decreases their adaptability to environmental change (Lin et al., 2008; Norberg et al., 2001), and creates growing sanitary risks resulting from strong selective pressures on pathogens and herbivores (Hoisington et al., 1999; Villareal and Lannou, 2000). In contrast, in-field genetic diversity would help prevent diseases (De Vallavieille-Pope, 2004; Zhu et al., 2000) as well as herbivore damage (Andow, 1991; Tooker and Frank, 2012). In addition, when combined to local participatory seed production, a practice that also attracts renewed interest even in developed countries (Dawson et al., 2011; Enjalbert et al., 2011; Osman and Chable, 2009), in-field genetic diversity would maintain the evolutionary potential of crop varieties, allowing them to adapt to their local environment (including co-evolving flora, fauna and pathogens). Here, we have shown that an increase in crop genetic diversity can also improve biodiversity, which is a general aim of all signatories to the Convention on Biological Diversity, and may help slow down the functional homogenization of agroecosystems. In view of the widespread positive relationship between species diversity and ecosystem functioning (e.g. Cardinale et al., 2012), a higher diversity of taxonomic groups such as soil microarthropods (springtails) and generalist predators (spiders and carabids) may result in better ecosystem services such as soil regeneration or biological control (Hajjar et al., 2008; Whittingham, 2011), but this remains to be demonstrated.

Although the impact of crop genetic diversity on farmland communities documented in the present study may appear moderate compared to that of chemical inputs or natural habitat loss, two major causes of biodiversity loss in agroecosystems (Tschamtké et al., 2005), it may nonetheless have significant positive impacts on biodiversity if implemented on a large scale (Macfadyen and Bohan, 2010), which would be easy for farmers. This raises the issue of extrapolating results of small-scale experiments to more natural systems: Hughes et al. (2008), for example, fear that the effects of genetic diversity observed in controlled, small-scale experiments will be masked by other factors in natural situations. However, this experiment was set-up in a real agricultural landscape and met the conditions identified by Hughes et al. (2008) as the requirements for genetic diversity to efficiently drive ecological processes: (1) crops are dominant in fields and therefore can be considered as foundation species; (2) genetic diversity in crop fields is controlled by farmers only and can be stable across time; (3) farmland communities are submitted to repeated anthropogenic disturbance, so that species and genetic diversity may be crucial for disturbance response and stability.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.03.004>.

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