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Positive effects of wheat variety mixtures on aboveground arthropods are weak and variable.

Florence Dubs^{a,b,*,*}, Alan Vergnes^{a,c,*}, Emilie Mirlicourtois^{a,b}, Isabelle Le Viol^a, Christian Kerbirou^a, Jérémie Goulnik^a, Soumaya Belghali^a, Laure Bentze^a, Sébastien Barot^b, and Emmanuelle Porcher^a

^aCentre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France

^bInstitut d'Ecologie et des Sciences de l'Environnement de Paris (IEES), Sorbonne Université, IRD, CNRS, INRA, P7, UPEC, Paris, France

^cCentre d'Ecologie fonctionnelle et Evolutive (CEFE), Univ Paul Valéry Montpellier 3, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

* **Corresponding author:** Tel.: +33(0)148027941; fax: +33(0)148027949

E-mail address: florence.dubs@gmail.com (F. Dubs).

^o These authors contributed equally to this work.

Highlights

- Wheat variety mixtures have contrasting effects on aboveground arthropod communities
- Wheat intraspecific diversity have a weak positive effect on predator abundances
- Wheat intraspecific and functional diversity have a weak negative effect on spider evenness

- Few wheat stand characteristics have effects on ground or rove beetles

Abstract

Although modern agriculture generally relies on homogeneous varieties that are usually grown in pure stands, crop variety mixtures have been used for a long time, notably to improve resistance to fungal diseases. A growing number of studies suggest that intraspecific plant diversity may also enhance the abundance and diversity of wild species and thereby some ecosystem services such as biological control by natural predators. However, positive effects of the genetic diversity of plant species on the diversity of associated communities have mostly been documented in natural systems, with only a handful of studies targeting crop species in agroecosystems. Here, we investigated the ecological effects of the number of winter wheat varieties (*Triticum aestivum*) on aboveground arthropods and particularly predatory species. We manipulated the number of wheat varieties (1, 2, 4 or 8) in 120 plots (80 m² each) to examine how wheat diversity and stand characteristics impact communities of three dominant aboveground arthropod groups that include many predatory species: ground beetles, rove beetles and spiders. The number of wheat varieties had a weak, but positive effect on predator abundance, notably spider abundance. In contrast, wheat functional diversity, as assessed by the number of wheat functional groups, was only negatively related to the diversity of spiders. Among wheat stand characteristics, the variance in plant height, wheat biomass and the Green Area Index were weakly correlated with ground beetle, rove beetle and predatory diversity, respectively. The Green Area Index was also weakly correlated with ground beetle abundance. Our study suggests that wheat variety mixtures have variable and limited effects on aboveground arthropods and probably low effectiveness to enhance biological control, but these results should be further tested under low-input agriculture in real fields.

Keywords: cultivar mixtures, farmland biodiversity, ground beetles, plant-insect interactions, rove beetles, spiders, winter wheat.

Introduction

Intensive agriculture is based on substantial use of synthetic inputs such as pesticides, combined with high-yield, genetically homogeneous varieties that are usually grown in pure stands, *i.e.* with a single variety per field (Gaba *et al.*, 2015). Such cropping systems are still widely used because of their high productivity but are now often considered unsustainable, at least because of side effects of inputs (*e.g.* impacts of pesticides on non-targeted species) and the dependence on fossil fuels (Shennan, 2008). Moreover, there are hints that crop yields are now plateauing after several decades of steady increase (Lobell *et al.*, 2011). Alternative agricultural practices are thus developing and many authors plead for the application of ecological and evolutionary knowledge to agriculture (Loeuille *et al.*, 2013; Gaba *et al.*, 2018). Of particular interest is the use of both interspecific and intraspecific crop diversity in the field (Mijatović *et al.*, 2013). Because low species and genetic diversities often lead to a low resilience to environmental changes, questions arise about the opportunity to go on using genetically homogeneous monocultures in an era of rapid global change (Tilman *et al.*, 2001). Numerous ecological studies on communities of wild plants suggest that increasing plant species or genetic diversity tends to improve ecosystem functioning (Hughes *et al.*, 2008). The most documented effect of plant species diversity and genetic diversity is an increase in primary production, total plant biomass (Cook-Patton *et al.*, 2011; Hajjar *et al.*, 2008) and in the stability of primary production through time (Nyfeler *et al.*, 2009; Tilman & Downing, 1996). The positive relationship between plant diversity and productivity is caused by a combination of complementarity (*i.e.* decrease in competition among individual plants) and

selection effects (Prieto *et al.*, 2015) that can also stabilize production through differences between species or genotypes in their response to environmental conditions and perturbations (Loreau & Mazancourt, 2013). This benefit of within-field cultivated diversity explains the recent regain of interest for agricultural practices such as intercropping or variety mixtures (Barot *et al.*, 2017, Gaba *et al.*, 2015), both of which potentially allowing the use of lower amounts of fertilizers.

Crop diversity, particularly variety mixtures, can also lower the use of pesticides, via an increase in resistance to pathogens (Finckh *et al.*, 2000) and perhaps in the abundance and diversity of predatory arthropod species present in the field (Ratnadass *et al.*, 2012; Siemann *et al.*, 1998). The role of natural predators as potential biological control agents in variety mixtures has been recognized only recently. Experimental approaches in biodiversity-ecosystem functioning (reviewed by Cook-Patton *et al.*, 2011) and community genetics (Hersch-Green *et al.*, 2011) have demonstrated that the positive effects of plant diversity on plant biomass can cascade through trophic levels and result in a larger biomass of herbivores and predatory species (Yee & Juliano, 2007). This effect can be caused by a general increase in resource availability for consumers and has been coined the “more individuals” hypothesis (Srivastava & Lawton, 1998). Alternatively, plant diversity may also lead to more diverse arthropod communities via an increase in the diversity of available resources (food or habitats, “more diversity” hypothesis, Southwood *et al.*, 1979).

Although the relationship between plant genetic diversity and arthropod communities has been extensively explored in natural systems, few studies have examined the effect of crop diversity on communities of aboveground arthropods (but see Chateil *et al.*, 2013; Crutsinger *et al.*, 2006). However, a number of aboveground arthropod groups found in cultivated fields include predatory species that may act as biological control agents. Among them, ground beetles, rove beetles and spiders represent an important part of the aboveground generalist

predators (Scheu, 2002) and their role as biological control agents has been recognized (Andersen *et al.*, 1983; Bryan & Wratten, 1984; Harwood *et al.*, 2001; Hatteland *et al.*, 2010; Kromp, 1999; Lang, 2003; Nyffeler & Sunderland, 2003; Symondson, 2004). By analogy with the well documented effects of vegetation on arthropods (reviewed by Langellotto & Denno, 2004; Tews *et al.* 2004), we have the following expectation: (1) The abundance of ground-dwelling arthropods should increase with indices of wheat biomass or leaf area, which can be seen as a proxy for primary resources, with potential cascading effects along food chains, from herbivores to predators. Such effects would be consistent with the “more individuals” hypothesis (Srivastava & Lawton, 1998). (2) Variance in stem height should enhance the diversity of ground-dwelling arthropods due to its positive effects on microclimatic and habitat diversity as demonstrated for rove beetles (Bohac, 1999), ground beetles (Langellotto & Denno, 2004; Brose, 2003) and cursorial spiders (Tews *et al.* 2004). Such effects would be consistent with the “more diversity” hypothesis.

Here, we used an experimental approach at the field scale to assess the effect of intraspecific crop diversity and stand characteristics on aboveground arthropod communities, with a focus on predatory species. We studied bread wheat (*Triticum aestivum*) as the dominant crop in northern France, and examined whether the identity and number of wheat varieties, hence the wheat stand characteristics, affected the diversity and abundance of predatory arthropods in the field.

Materials and methods

Site location, pedoclimatic conditions and experimental design

The field site was located at the French National Institute for Agricultural Research experimental station in Versailles, France (48°81' N, 2°09' E, Fig. 1A). The experimental station is surrounded by hedgerows and neighbored by woody patches on the northern side. The field site is surrounded by grassy paths.

Sixteen *T. aestivum* (winter wheat) varieties were used for the experiment. These varieties were chosen from an initial collection of 57 varieties representing different breeding histories (from local landraces to modern elite varieties) and a large diversity of above- and belowground morphological, phenological and physiological traits. The 57 varieties were classified into four “functional groups” on the basis of their traits using ascending hierarchical classification (see Appendix A for details). Four varieties were chosen within each functional group for the field experiment. In a 2.6 ha field, 120 plots were randomly chosen (Fig. 1B) to be seeded with 1, 2, 4, or 8 varieties, with respectively 48 (three replicates of each monoculture), 24, 28 and 20 replicates for each number of varieties. We also varied the number of functional groups for each number of varieties above 1: there were “homogeneous” (a single functional group) vs. heterogeneous (two or more functional groups) mixtures (see Appendix A for the list of all variety mixtures). Functional group mixtures were therefore replicated in the experimental site, while variety mixtures were not. In November, all plots were sown with 250 g of seeds per m². Varieties in a mixture were seeded in equal densities. All plots were of identical size (10.5 m x 8.0 m) except three monoculture plots that were halved in size (10.5 m x 4 m) due to limited seed availability. This size difference was, however, not a major issue because monocultures were replicated thrice, such that we could check that the small-size plots were not outliers. Each plot was buffered from adjacent plots or the field edge by a 1.75 m-wide row of triticale (*x Triticosecale*, Fig. 1C). The plots were managed conventionally, but with relatively low input levels. At the beginning of measurements, all plots had received one herbicide spray (Archipel® and Harmony Extra®) in mid-March and relatively low doses of a nitrogen fertilizer (ammonium-nitrate) applied in February (40 kgN.ha⁻¹) and mid-April (80 kgN.ha⁻¹).

Wheat stand characteristics

In each plot, several stand characteristics likely influencing the presence and abundance of

arthropods were measured: wheat biomass, the Green Area Index (GAI) and the mean and variance of plant height in the mixture. The GAI, an index of vegetation cover, was measured in May 2015 using the gap fraction method (hemispherical photography, Baret *et al.*, 2010). In June 2015, wheat biomass was harvested at the onset of flowering in sub-plots of 50 x 52.5 cm centred on three rows by uprooting whole plants. Roots were separated from shoots and samples were dried 72 hours at 65 °C and weighed. At the same time, the height of 10 wheat stalks was measured in the field to obtain the mean and coefficient of variation of plant height in each plot.

Sampling and identification of aboveground arthropods

Aboveground arthropods were sampled during the peak of activity of most western European species (Lövei & Sárospataki, 1990), May 5-18 2015. Exposure time of about 15 days is commonly used in the study of soil aboveground arthropods in agricultural environments (Bohan *et al.*, 2011; Chateil *et al.*, 2013; Schmidt *et al.*, 2006; Vergnes *et al.*, 2013). One plastic pitfall trap (8 cm diameter, 500 cm³, half-filled with propylene glycol) was dug into the ground with its rim flush with the ground surface in the centre of each plot. Propylene glycol is a preservative solution that is neither attractive nor toxic to invertebrates (Thomas, 2008). A plastic roof (10 x 10 cm) was installed at approximately 2 cm above each pitfall trap to prevent rain and debris from entering the traps.

All spiders, adult ground beetles (Carabidae) and adult rove beetles (Staphylinidae) were identified to species level where possible, except for immature spiders, which were identified to morphospecies level and *Aleocharinae* individuals (45% of total rove beetles), which were identified to subfamily level only (hereafter *Aleocharinae* spp). Spiders were identified using the keys of Roberts (2001), ground beetles with the keys of Roger *et al.* (2013) and Hürka (1996) and rove beetles with the keys of Lot (2009) and Freude *et al.* (1964). Contrary to spiders that are all predatory, ground beetles and rove beetles have various diets: predatory,

phytophagous, detritivore or polyphagous (Bohac, 1999; Laroche, 1990). Predatory species were identified using various bibliographic sources (see Appendix B: Table S1 for details).

Data analysis

Aboveground arthropod communities in each plot were characterized by (1) the abundance (number of individuals) of each species observed, (2) the total number of species observed (species richness) and (3) the evenness of species abundances using Pielou's index (Shannon index $1/\log(\text{species richness})$), (Vegan package, Oksanen *et al.*, 2016). These three types of response variable were calculated for each taxonomic group of aboveground arthropods separately (ground beetles, rove beetles and spiders) and for the phylogenetically heterogeneous group of predatory species including all spiders and exclusively predatory ground and rove beetle species.

On each of these three response variables, we tested the impact of different types of variables characterizing crop diversity and composition, (1) the number of wheat varieties (a proxy for crop genetic diversity), (2) the number of wheat functional groups (a proxy for crop trait diversity) and (3) the stand characteristics GAI, shoot biomass, the mean and the coefficient of variation of plant height. For all models, the spatial coordinates (longitude and latitude) of plots were included to account for the possibility of spatial gradients in arthropod community characteristics due to border effects.

Analyses were conducted in three steps. First, the effects of the number of wheat varieties were tested (\sim Longitude + Latitude + Number of wheat varieties). Second, the effects of the number of functional groups were tested in separate models (\sim Longitude + Latitude + Number of functional groups) because of its correlation with the number of wheat varieties (Fig. 2). Finally, the effects of wheat stand characteristics were tested simultaneously in a single model (\sim Longitude + Latitude + Wheat biomass + Mean plant height + Variance of plant height + GAI) but without including the number of varieties or the number of functional

groups because of correlations between stand characteristics and numbers of varieties or functional groups (Fig. 2). In models analysing wheat mixture characteristics, forward model selection was applied using the AIC (Akaike Information Criterion) before testing the significance of effects and the goodness of fit.

Depending on the type of response variable, we used three types of statistical models. For species richness, we used generalized linear models (GLMs) with a Poisson error distribution (Crawley, 2009) and checked for overdispersion (Cameron & Trivedi, 1990). Because the number of species observed in a sample is known to increase with the number of individuals sampled (Gotelli & Colwell, 2011), the total abundance was added as a fixed covariate in the model to partly disentangle species richness from total abundance. This partly allowed us to test the “more diversity” hypothesis, under which we expect more invertebrate species associated with more wheat varieties, all else being equal (in particular, with the same total abundance). We checked that there were no multicollinearity issues between explanatory variables (squared variance inflation factors (VIF) < 2 , Zuur *et al.*, 2010). To study the abundance of species, the abundances of all species were studied together in a single model. We used only species observed in at least ten percent of samples in order to avoid issues related to different distributions among species and the ensuing zero inflation in GLMM, (Zuur *et al.* 2012), including species identity as a random effect to control for differences in abundance across species. To do so we used mixed models (GLMMs) with Poisson error or negative binomial error distribution (Bolker *et al.*, 2009) and checked for overdispersion with the `overdisp_fun` function (<http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html>). In GLMMs, the best fit between Poisson, negative binomial, zero-inflated Poisson and zero-inflated negative binomial models was selected on the basis of the AIC. Finally, for the Pielou index, the rank-transformation (Akritas, 1990) was applied to reach a normal distribution of residuals and then analysed with linear models (LMs). When the normality was still not

verified, we used a Kruskal-Wallis test.

The significance of effects was calculated using type II sums of squares for unbalanced designs (Bolker *et al.*, 2009). The goodness of fit of each model was calculated as an adjusted R^2 for LMs, conditional R^2 (the total variance explained by random and fixed effects) and marginal R^2 (the variance explained by fixed effects alone) for GLMMs, and a pseudo R^2 for GLMs.

All data analyses were performed using the R software (version 3.4.1, R Development Core Team, 2017) and the car (for unbalanced design, Fox & Weisberg, 2011), lme4 and glmADMB (for GLMMs, Bates *et al.*, 2015; Fournier *et al.*, 2012; Skaug *et al.*, 2016), MuMin (for forward model selection, Barton, 2017), piecewiseSEM (to compute coefficient of determination for GLMMs, Lefcheck, 2015) and AER (for GLM overdispersion test, Kleiber & Zeileis, 2008) packages.

Results

Description of aboveground arthropod communities and wheat stands

Overall, 86 species were captured (1271 individuals from 25 species for ground beetles, 1436 individuals from 25 morphospecies of rove beetles and 542 individuals from 36 morphospecies for spiders), 67 of which were predatory. In each group, the most abundant species are commonly observed in European agroecosystems. The number of wheat varieties and the number of functional groups were highly correlated (Spearman correlation coefficient = 0.84). The number of wheat varieties was positively correlated with the mean and coefficient of variation of wheat height (0.23 and 0.72, respectively). The number of functional groups was also positively related to the mean and coefficient of variation of wheat height (0.22 and 0.73, respectively) but negatively correlated with wheat shoot biomass (-0.21). Wheat shoot biomass was negatively correlated with the coefficient of variation of the

height of wheat stalks (- 0.21) but positively correlated with the GAI (0.22). Finally, the mean and coefficient of variation of the height of wheat stalks were positively correlated (0.30) (Fig. 2).

Effect of wheat intraspecific diversity on the abundance and diversity of aboveground arthropod communities

Overall, wheat diversity had limited effect on aboveground arthropods, which differed across taxonomic groups and species within a group (see Appendix B: Tables S5-S8 for detailed values across wheat diversity treatments). The number of wheat varieties had a positive, but small effect on spider abundance ($\beta = 0.052 \pm 0.023$, $P = 0.027$, marginal $R^2 = 0.051$, see Appendix B: Table S2). This effect was variable across species, with the most impacted species being *Oedothorax apicatus*, *Tenuiphantes tenuis*, *Erigone atra*, *Oedothorax retusus* and *Pardosa prativaga* (Fig. 3). These species are among the most abundant species and all belong to the *Linyphiidae* family with the exception of *P. prativaga* (*Lycosidae*) (Appendix B: Fig. S1C). Most likely as a result of the increased abundance of dominant species, the number of varieties had a negative effect on the evenness of spiders (i.e. Pielou index, $\beta = - 0.20 \pm 0.10$, $P = 0.038$, adjusted $R^2 = 0.09$, see Appendix B: Table S3A). The number of wheat varieties also had a positive, but small effect on predator abundance ($\beta = 0.025 \pm 0.010$, $P = 0.012$, marginal $R^2 = 0.012$, see Appendix B: Table S2). This effect was variable across species, with the most affected taxa being the two most abundant rove beetle taxa: *Aleocharinae* spp, and *Tachyporus hypnorum* and the three most abundant ground beetle species *Poecilus cupreus*, *Phyla obtusa* and *Clivina fossor* (Fig. 4, Appendix B: Figs. S1A and B). In contrast, none of the other aboveground arthropods (ground beetles or rove beetles) were impacted by the number of wheat varieties, regardless of the dependent variable considered (species abundance, richness or evenness) (see Appendix B: Tables S2 and S4). Finally, the number of wheat functional groups, a proxy for trait diversity, also had a limited

effect on aboveground arthropods with only a negative effect on the evenness of spiders ($\beta = -0.22 \pm 0.10$, $P = 0.026$, adjusted $R^2 = 0.1$, see Appendix B: Table S3A).

Effects of wheat stand characteristics

The characteristics of wheat stands had in some cases an effect on the diversity of arthropods, but never on their abundance (see Appendix B: Table S5 for detailed values across wheat diversity treatments). Wheat shoot biomass had a positive effect on the evenness of ground beetles (Pielou index, $\beta = 0.31 \pm 0.09$, $P = 0.001$, adjusted $R^2 = 0.10$, see Appendix B: Table S3A) and predators as a whole ($\beta = 0.23 \pm 0.09$, $P = 0.012$, adjusted $R^2 = 0.05$, see Appendix B: Table S3A), while the GAI had a positive effect on ground beetle abundance ($\beta = 0.082 \pm 0.042$, $P = 0.050$, marginal $R^2 = 0.019$, see Appendix B: Table S2) and on rove beetle species richness ($\beta = 0.221 \pm 0.102$, $P = 0.039$, pseudo $R^2 = 0.31$, see Appendix B: Table S4) and the variance of plant height had a negative effect on the evenness of rove beetles (Pielou index, $\beta = -0.21 \pm 0.09$, $P = 0.017$, adjusted $R^2 = 0.12$, see Appendix B: Table S3A).

Weak signal of wheat mixture but stronger border effects

In addition to the few and generally weak effects of the crop ($0.025 < |\beta| < 0.307$), there was a stronger North-South gradient ($0.139 < |\beta| < 0.309$) in the abundance and diversity of arthropod communities, with significantly more individuals and less even abundances at the northern end of the field site (significant positive, respectively negative “latitude” effect, Tables S2-S4), which lies closer to the woody patches (Figs 1A and B). Longitude had also, in fewer cases, a significant but weak negative effect (see Appendix B: Tables S2 and S4).

Discussion

Our experiment manipulated wheat intraspecific diversity and combinations of wheat traits to examine their impact on aboveground arthropods, with a focus on predatory species. We observed limited effects that can be summarized as a positive effect of the number of varieties

on the abundance of the most common spider species, as well as on the abundance of the most common predatory species (ground and rove beetles) and a few more significant relationships between wheat stand characteristics and (1) the abundance of ground beetles, (2) predators as a whole, (3) the diversity of ground and rove beetles and (4) the diversity of exclusive predator communities. Below, we discuss how these results compare to similar experiments in more natural settings, and whether crop variety mixtures can be expected to improve biological control in agroecosystems.

Positive effect of wheat intraspecific diversity on several spider species and consequences on spider diversity

The observation of an increased abundance of several spider species in plots with multiple varieties is consistent with previous experiments examining the effect of the genetic diversity of plant species on arthropod communities, although the mechanisms involved may differ. For example, Crutsinger *et al.* (2006) in *Solidago altissima*, Moreira and Mooney (2013) in *Baccharis salicifolia*, Abdala-Roberts *et al.* (2016) in *Phaseolus lunatus* or Chateil *et al.* (2013) in *T. aestivum* showed that higher plant genetic diversity was associated with higher abundance and/or species diversity of invertebrate taxa (mainly spiders). In our experiment, however, increased spider abundance was associated with decreased spider diversity (as indicated by a significant negative effect of the number of wheat varieties on the Pielou index, see Appendix B: Table S4). Although species diversity was not always measured with the same indices, this pattern contrasts with most previous findings that plant genetic diversity tends to increase arthropod diversity (Chateil *et al.*, 2013; Crutsinger *et al.*, 2006; Moreira & Mooney, 2013).

Two main mechanisms are generally invoked to explain the positive relationship between plant genetic diversity and the abundance/diversity of invertebrates: (1) increased primary productivity resulting in more resources for herbivores and subsequently for the upper trophic

levels (“more individuals” hypothesis, Srivastava & Lawton, 1998), which may increase species diversity via sampling effects or (2) increased diversity of resources for herbivores or increased diversity of microhabitats for all groups (“more diversity” hypothesis, Southwood *et al.*, 1979). Here, this later mechanism is unlikely to be at play. First, wheat diversity was associated with decreased spider diversity (decreased evenness), whereas the opposite pattern is expected under the “more diversity” hypothesis. Second, we did not observe any significant relationship between spider abundance/diversity and wheat stand characteristics that are known to have a direct influence on spider communities. For example, complex vegetation structure is sometimes associated with increased spider abundance (Langellotto & Denno, 2004) via the diversity of available microhabitats. However, the variance in plant height within a plot, a proxy for the complexity of vegetation structure, was not related to spider abundance or diversity (see Appendix B: Tables S2-S4). Higher spider abundance in variety mixtures is therefore likely an indirect consequence of higher primary productivity, mediated by the abundance of herbivorous preys, although the evidence for this mechanism is mixed. For example, increasing the number of wheat varieties increased plant height, but not shoot biomass (Fig. 2).

The negative effect of intraspecific wheat diversity on spider evenness and the positive effect of intraspecific wheat diversity on spider abundance affecting preferentially the most abundant species may be explained by species-specific dispersal abilities. These abundant species were mostly *Linyphiidae* (*O. apicatus*, *T. tenuis* or *E. atra*, Fig. 3), which dominated spider communities, as is often the case in agroecosystems in northern-temperate Europe (Nyffeler & Sunderland, 2003). Linyphiids are small spiders (often less than 2 mm), which are capable of mass aerial dispersal (Bell *et al.*, 2005). This dispersal strategy, coupled with their rapid population growth during spring time (Roberts, 2001), allows *Linyphiidae* to move to and thrive in areas of the fields that offer suitable micro-local conditions and higher prey

densities (Harwood *et al.*, 2001). This may explain their higher sensitivity to wheat diversity than other spiders, also observed in Chateil *et al.* (2013). In our case, the effect of intraspecific wheat diversity seems limited to the more dispersive species, which are according to environmental filtering theory (Keddy, 1992) not filtered by landscape and so may colonize the experimental field and may spend more time foraging in the resourceful plots where they are captured in higher abundance. Species with lower dispersal ability may be absent from resourceful plots. This would be the case for wolf spiders (*Lycosidae*) (Blandenier, 2009), which are medium-sized predators (around 5 mm) capturing their prey by foraging on the ground. They were relatively frequent in our experimental site (as in Lang, 2003), but were less sensitive to crop diversity (except for *P. prativaga*).

Although the number of wheat varieties tended to increase the abundance of some spider species, the stand characteristics responsible for such effect were difficult to identify. This is exemplified first by the absence of a significant relation between any of the stand characteristics we studied and spider abundance, and second by the absence of a significant relationship between the number of wheat functional groups and spider abundance or species richness except evenness. Some authors have emphasized that trait or phenotypic diversity should matter more than genetic diversity *per se* in explaining the effects of plant species on their associated communities (Hersch-Green *et al.*, 2011; Hughes *et al.*, 2008). Yet, few studies have successfully identified traits responsible for the effects of genotypic diversity (Crustinger, 2016). Here, we used the number of functional groups as a proxy for phenotypic diversity: these groups of varieties were built on the basis of a large number of traits, covering components of plant shoot and root morphology, plant phenology, disease resistance, metabolism and yield. Because variety mixtures could contain more than one variety from the same functional group, the number of functional groups should have been a better driver of arthropod community abundance and diversity than the number of varieties. Yet the opposite

was observed. Besides, stand characteristics that had been chosen for their a priori expected effects on arthropods were poorly related to spider abundance and diversity. All these observations suggest that the most important stand characteristics and wheat traits driving the positive effect of the number of varieties on spider abundance remain to be identified.

An overall limited effect of crop diversity and composition on aboveground arthropods

Although we did detect a weak effect of intraspecific wheat diversity on spiders and on predatory species, in general the community of aboveground arthropods was little impacted by the number or functional diversity of wheat varieties in each plot, which conflicts with previous similar studies (see Crutsinger, 2016 for some examples). In some cases, the effect of plant genetic diversity on arthropod communities was even larger than the effect of interspecific plant diversity (Crawford & Rudgers, 2013). Assuming that there is no bias against negative results in the literature (but see Parker *et al.*, 2016), so that the large number of articles reporting a significant effect of plant genetic diversity are representative of its true impact in nature, the possible causes for the limited effect of crop genetic diversity on predator communities observed here can be manifold. Below we discuss three of the most likely causes that are related to the ecology of the organisms studied and to agricultural practices.

First, detecting an effect of plant (genetic) diversity on animal communities is a matter of appropriate spatial and temporal scales. The experiment should be designed such that the targeted taxonomic groups have ample time to reach their preferred plots and stay there or to multiply in the more favourable plots. In the case of an annual crop such as wheat, we were limited by crop rotation, such that the experiment could last no more than a few months at the maximum. As a result, the effects of wheat on arthropod communities were strongly dependent on the dispersal ability of the sampled organisms. We were also limited in plot size, with a strong trade-off between plot size and the number of replicates per mixture

treatment (*i.e.* number of varieties or functional groups). The size and time frame of this experiment was, however, comparable to other studies with a strong effect of genetic diversity on arthropod communities (*e.g.* Crutsinger *et al.*, 2006, 1 m²-plots, one growing season). Yet, whether the time frame of the experiment was sufficient to detect an effect of wheat diversity on arthropod communities depends on the dispersal ability of the regional pool of species. The aboveground arthropod species trapped in this study (spiders, ground beetles and rove beetles) are generally representative of communities observed in European farmland and, as such, are thought to be able to colonize and to thrive in an open and non-permanent habitat, ploughed and harvested every year (Eyre, 1994). Regardless of the alleged good dispersal abilities of the various species, the size and time frame of our experiment was long enough for all of the species to forage in or disperse to the plots. However, we detected a strong border effect on either the abundance or the diversity of all taxa, suggesting source/sink dynamics between the border and the centre of the field, within the time frame of our study. In either case, these phenomena limited the abundance of arthropods in the experimental plots and may have masked a possible effect of mixture treatments.

Second, if a plant species influences predatory arthropod communities through indirect, bottom-up effects, via *e.g.* more abundant or more diverse food sources for herbivorous preys, the bottom-up effects of both intra- and interspecific plant diversity on arthropods may be buffered down in higher trophic levels because of a top-down control by predators (Terborgh, 2015). Pitfall traps are not the best setup to assess herbivore abundance, because they also live on vegetation. Here the herbivores captured in the pitfall traps were not numerous enough to test whether the effect of the number of wheat varieties was stronger on herbivores or on predators and the possibility of a top-down control. However, several studies (*e.g.* Johnson *et al.*, 2006; Moreira & Mooney, 2013) did detect strong direct or indirect effects of plant genetic diversity on predators or parasitoids.

Third, most previous experiments on the impact of plant genetic diversity on arthropods were performed in ecological research stations (*e.g.* Abdala-Roberts *et al.*, 2016; Crutsinger *et al.*, 2006; Moreira & Mooney, 2013) or under organic farming (Chateil *et al.*, 2013), whereas this experiment was conducted under conventional farming, with moderate use of pesticides and fertilizers in the year of the experiment, but with a long history of more intensive farming in this agronomy research station. Intensive conventional farming is known to have strong negative effects on the abundance of most species and on the diversity of communities (see Kremen & Miles, 2012 for reviews; Pfiffner & Niggli, 1996) via the effects of synthetic inputs and ploughing (Bouthier *et al.*, 2014). We observed much lower abundances of spiders and ground beetles in this experiment under conventional farming than in an earlier comparable experiment with bread wheat under organic farming (Chateil *et al.*, 2013) and larger experimental plots but with a comparable sampling design: same period and duration of pitfall trapping (2-weeks trapping session in May, same density of pitfall traps): the mean (\pm standard error) number of individuals per trap in this experiment vs. Chateil *et al.*'s (2013) was 4.4 ± 0.3 vs. 25.6 ± 1.6 for spiders and 10.6 ± 0.4 vs. 38.9 ± 2.5 for ground beetles. In contrast, the number of rove beetles was similar in both experiments (12.0 ± 0.5 vs. 11.7 ± 0.75). With a single replicate per farming type, we cannot conclude that farming system is the main driver of such differences in abundances, but the trend is consistent with the widely demonstrated negative impact of conventional farming on biodiversity (Lichtenberg *et al.*, 2017). Nevertheless, the low number of arthropod individuals observed in this experiment has likely lowered our ability to detect an effect of crop variety mixtures on predator communities.

Conclusions

In general we found congruent, but much weaker effects of crop genetic diversity than in

previous similar studies: only a few spider species exhibited increased abundance when the number of wheat varieties increased, whereas ground and rove beetles were largely unaffected by the crop structure and diversity. In particular, the distance to the field edge had a stronger effect on arthropod communities than the crop itself, which is consistent with the well-documented general role of the landscape scale for aboveground arthropods and predation in farmland (Tscharrntke *et al.*, 2007). We were not able to conclude on the exact mechanism explaining the difference between our and previous studies, but part of the reason may be linked with conventional farming lowering the general abundance and diversity of arthropods in the field. Our results therefore suggest that wheat variety mixtures are unlikely to benefit aboveground arthropods, hence to improve biological control, under conventional farming. However this prediction needs to be tested with new experiments directly comparing the impact of the same mixtures between conventional farming, low-input farming and organic agriculture. Finally, further investigations are also needed to upscale the study of crop variety mixtures and examine whether within-field genetic diversity has stronger positive impacts on the diversity and abundance of arthropod predators on the longer term or at the farm scale, as suggested by Cardinale *et al.* (2011).

Authors' Contributions

S. Ba. and E. P. contributed to the experimental design; S. Ba., L. B., J. G, E. M. and A. V. collected the data; S. Be., J. G., I. L. V., E. M., and A. V. identified the aboveground arthropods; A. V, E. M. and F. D. analysed the data set; E. P. and C. K. assisted in the data analysis; S. Ba., F. D., E. P., and A. V. wrote the paper; C. K. and I. L. V. made valuable comments on the writing. All authors contributed critically to the drafts and gave final approval for publication.

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Figures

Fig. 1. Location of field site (A) and plot distribution (B) in the experimental station of the French National Institute for Agricultural Research, in Versailles, France (48°81' N, 2°09' E). Each plot was buffered by a 1.75 m-wide row of triticale (C).

Fig. 2. Spearman correlations between the number of wheat varieties, the number of functional groups and wheat stand characteristics (PerformanceAnalytics package, Peterson et al. 2014). The distribution of each variable is shown on the diagonal. In the lower triangle, bivariate scatter plots with a fitted line are displayed. In the upper triangle, the corresponding Spearman correlation coefficients are given. Significance levels are as follows: $P < 0.001$ (***), $0.01 < P < 0.05$ (*), $0.05 < P < 0.1$ (.).

Fig. 3. Predicted abundance of spider species as a function of the number of wheat varieties. The dots and the lines are the values predicted by the generalized linear mixed-effect model including number of wheat varieties, latitude and longitude as explanatory variables.

Fig. 4. Predicted abundance of predatory species as a function of the number of wheat varieties. Species names of ground beetles are in bold and rove beetles are underlined. Note that the spider species are the same as on Fig. 3, because all spiders are predators. The dots and the lines are the values predicted by the generalized linear mixed-effect model including number of wheat varieties, latitude and longitude as explanatory variables.

Fig. 1.

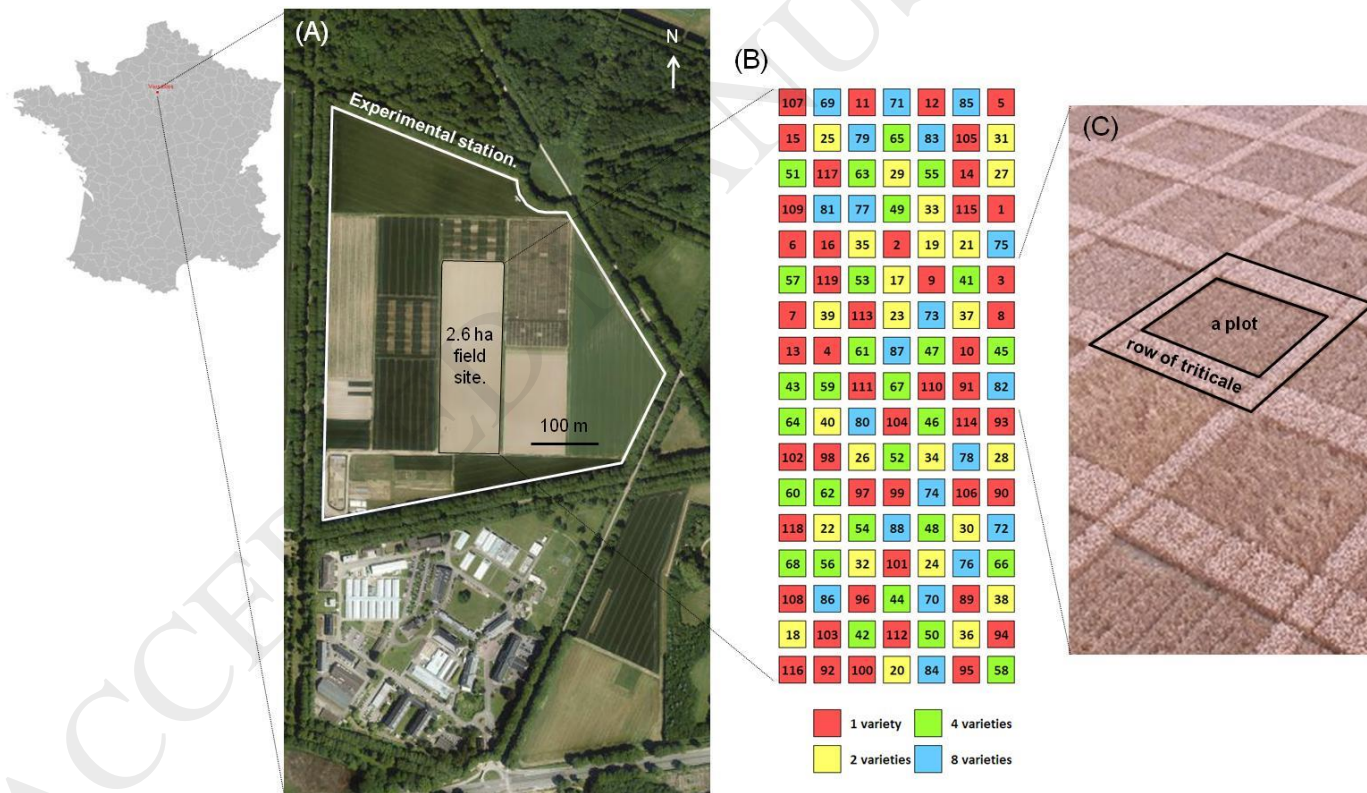


Fig. 2.

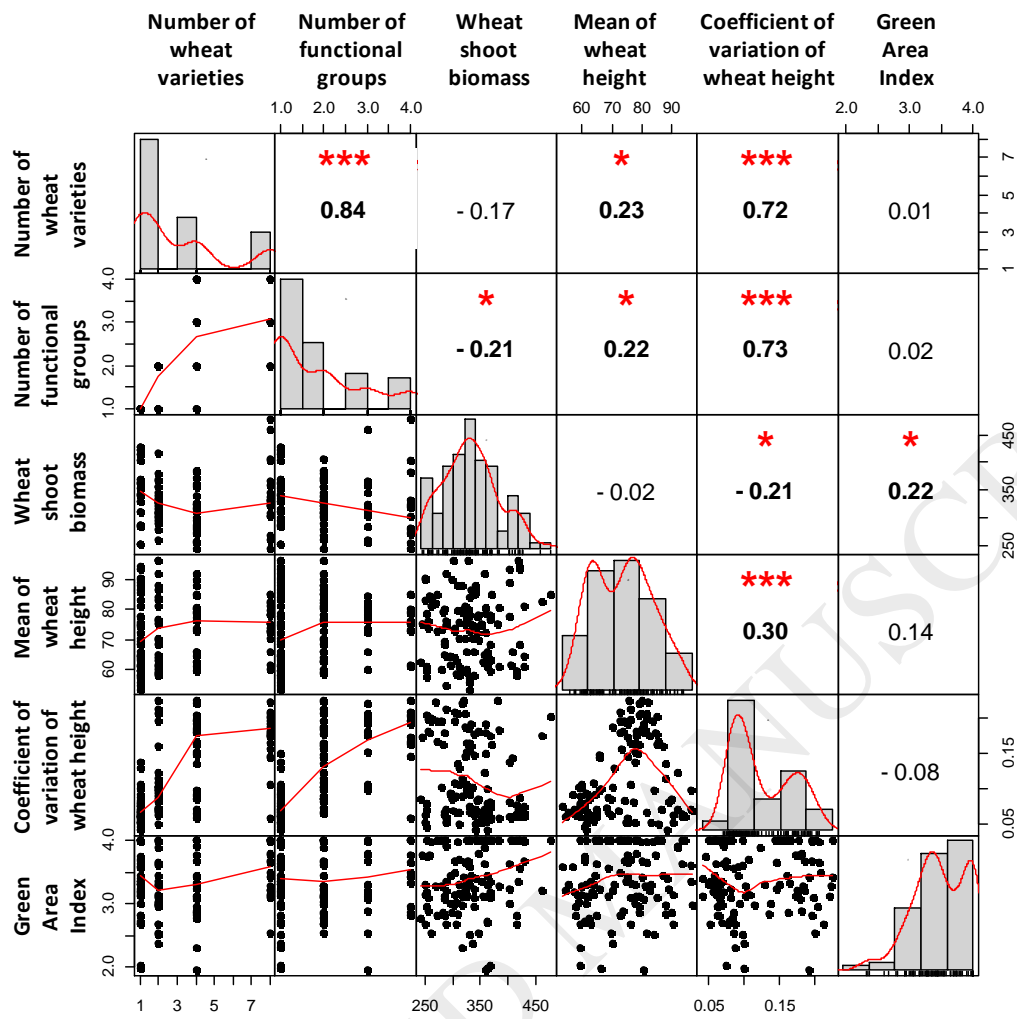


Fig. 3.

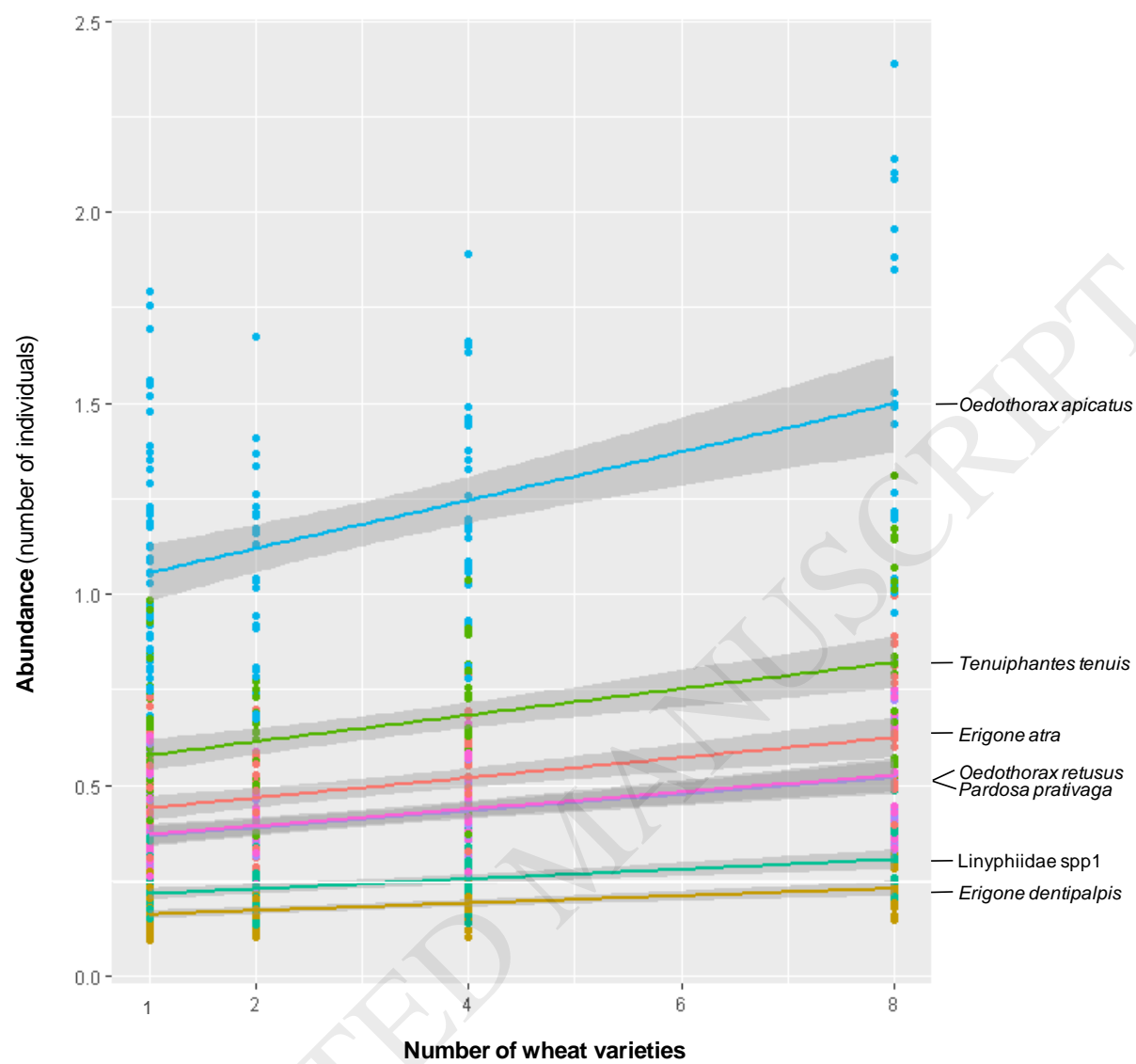


Fig. 4.

