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

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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 m^2 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

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Introduction

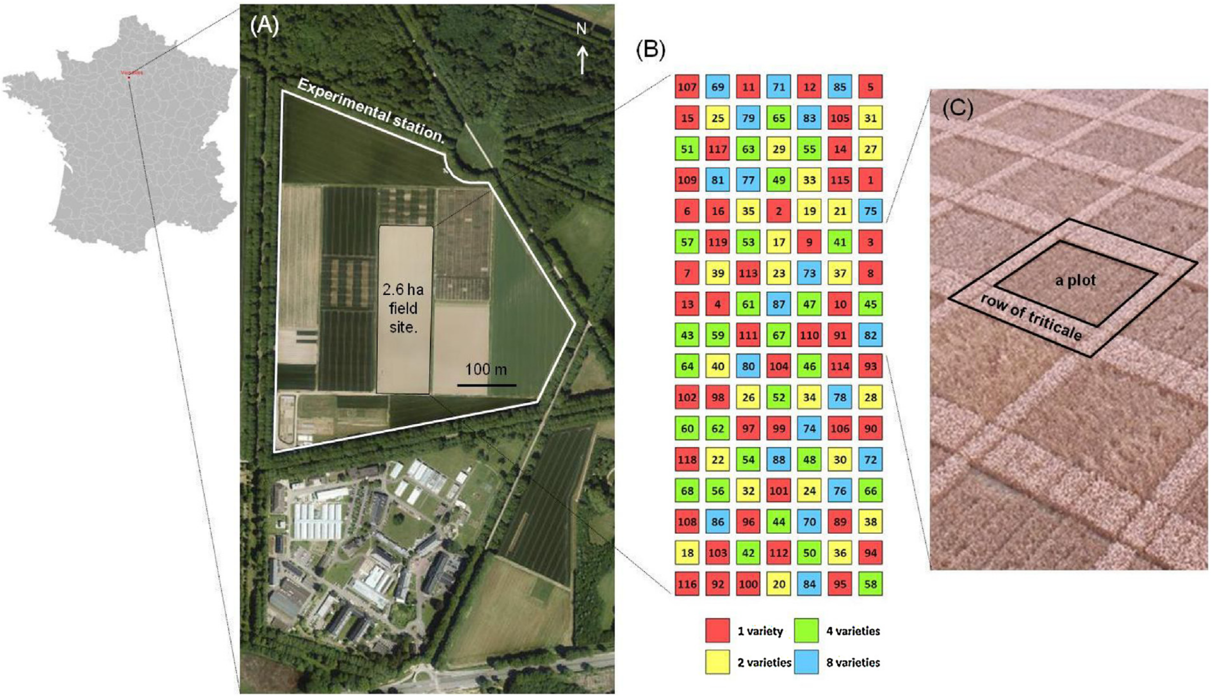
Intensive agriculture is based on substantial use of synthetic inputs such as pesticides, combined with high-yield, genetically homogeneous varieties that are usually grown in pure stands, *i.e.* with a single variety per field (Gaba et al. 2015). Such cropping systems are still widely used because of 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, Schlenker, & Costa-Roberts 2011). Alternative agricultural practices are thus developing and many authors plead for the application of ecological and evolutionary knowledge to agriculture (Loeuille, Barot, Georgelin, Kylafis, & Lavigne 2013; Gaba et al. 2018). Of particular interest is the use of both interspecific and intraspecific crop diversity in the field (Mijatović, Van Oudenhoven, Eyzaguirre, & Hodgkin 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, Inouye, Johnson, Underwood, & Vellend 2008). The most documented effect of plant species diversity and genetic diversity is an increase in primary production, total plant biomass (Hajjar, Jarvis, & Gemmill-Herren 2008; Cook-Patton, McArt, Parachnowitsch, Thaler, & Agrawal 2011) and in the stability of primary production through time (Tilman & Downing 1996; Nyfeler et al. 2009). 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 (Gaba et al. 2015; Barot et al. 2017), 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 (Siemann, Tilman, Haarstad, & Ritchie 1998; Ratnadass, Fernandes, Avelino, & Habib 2012). 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, Turley, & Johnson 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, Brown, & Reader 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 Crutsinger et al. 2006; Chateil et al. 2013). 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, Hansen, Rydland, & ØYre 1983; Bryan & Wratten 1984; Kromp 1999; Harwood, Sunderland, & Symondson 2001; Lang 2003; Nyffeler & Sunderland 2003; Symondson 2004; Hatteland et al. 2010). 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.



🟥 107	🟦 69	🟥 11	🟦 71	🟥 12	🟦 85	🟥 5
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🟩 51	🟥 117	🟩 63	🟨 29	🟩 55	🟥 14	🟨 27
🟥 109	🟦 81	🟦 77	🟩 49	🟨 33	🟥 115	🟥 1
🟥 6	🟥 16	🟨 35	🟥 2	🟨 19	🟨 21	🟦 75
🟩 57	🟥 119	🟩 53	🟨 17	🟥 9	🟩 41	🟥 3
🟥 7	🟨 39	🟥 113	🟨 23	🟦 73	🟨 37	🟥 8
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🟩 43	🟩 59	🟥 111	🟩 67	🟥 110	🟥 91	🟦 82
🟩 64	🟨 40	🟦 80	🟥 104	🟩 46	🟥 114	🟥 93
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🟩 60	🟩 62	🟥 97	🟥 99	🟦 74	🟥 106	🟥 90
🟥 118	🟨 22	🟩 54	🟦 88	🟩 48	🟨 30	🟦 72
🟩 68	🟩 56	🟨 32	🟥 101	🟨 24	🟦 76	🟩 66
🟥 108	🟦 86	🟥 96	🟩 44	🟦 70	🟥 89	🟨 38
🟨 18	🟥 103	🟩 42	🟥 112	🟩 50	🟨 36	🟥 94
🟥 116	🟥 92	🟥 100	🟨 20	🟦 84	🟥 95	🟩 58

🟥 1 variety
🟩 4 varieties
🟨 2 varieties
🟦 8 varieties

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).

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 neighboured 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 Supplementary 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 Supplementary 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 m^2. Varieties in a mixture were seeded in equal densities. All plots were of identical size (10.5 m × 8.0 m) except three monoculture plots that were halved in size (10.5 m × 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 (×*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, de Solan, Lopez-Lozano, Ma, & Weiss 2010). In June 2015, wheat biomass was harvested at the onset of flowering in sub-plots of 50 × 52.5 cm centred on three rows by uprooting whole plants. Roots were separated from shoots and samples were dried 72 h 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 (Schmidt, Clough, Schulz, Westphalen, & Tscharntke 2006; Bohan, Boursault, Brooks, & Petit 2011; Chateil et al. 2013; Vergnes, Pellissier, Lemperiere, Rollard, & Clergeau 2014). One plastic pitfall trap (8 cm diameter, 500 cm^3, 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 × 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, Jambon, and Bouger (2013) and Hůrka (1996) and rove beetles with the keys of Lott (2009) and Freude, Harde, and Lohse (1964). Contrary to spiders that are all predatory, ground beetles and rove beetles have various diets: predatory, phytophagous, detritivore or polyphagous (Larochelle 1990; Bohac 1999). Predatory species were identified using various bibliographic sources (see Supplementary 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/log(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 (∼Longitude + Latitude + Number of wheat varieties). Second, the effects of the number of functional groups were tested in separate models (∼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 (∼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, Ieno, & Elphick 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, Saveliev, & Ieno 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

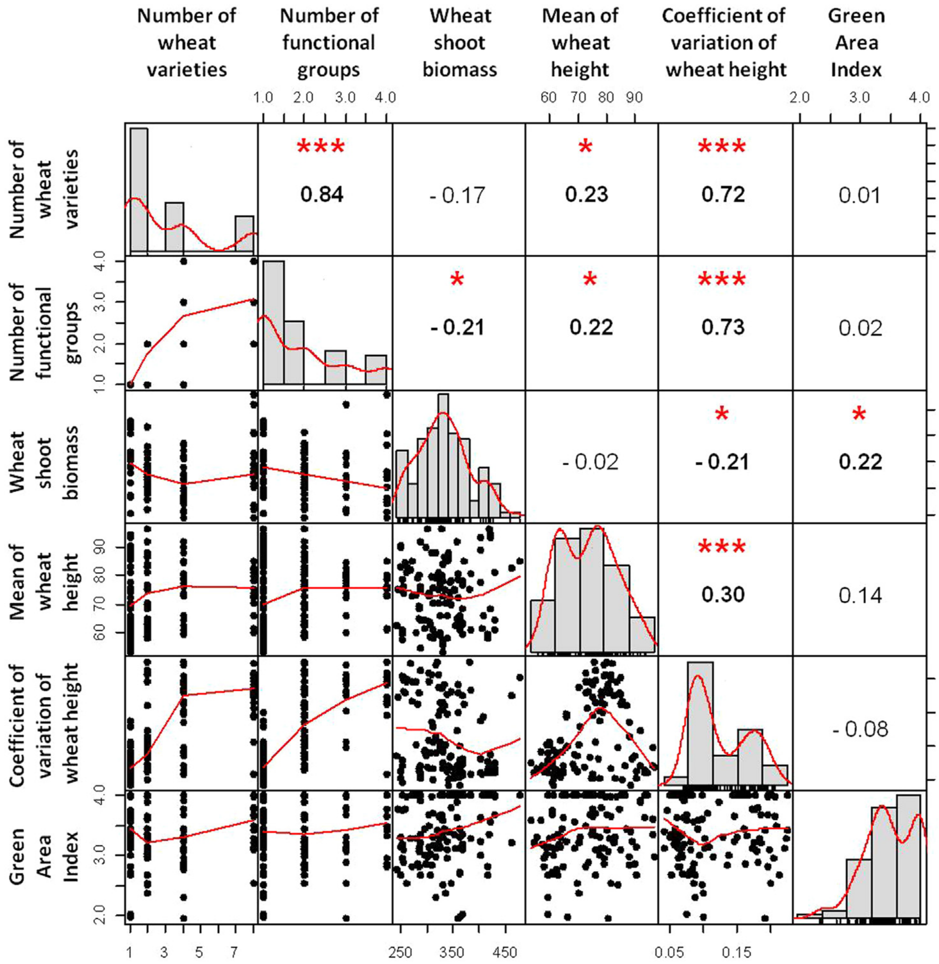

Fig. 2. Spearman correlations between the number of wheat varieties, the number of functional groups and wheat stand characteristics (PerformanceAnalytics package, Peterson et al. 2014). The distribution of each variable is shown on the diagonal. In the lower triangle, bivariate scatter plots with a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

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, Fournier et al. 2012; Bates, Maechler, Bolker, & Walker 2015; Skaug, Fournier, Bolker, Magnusson, & Nielsen 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

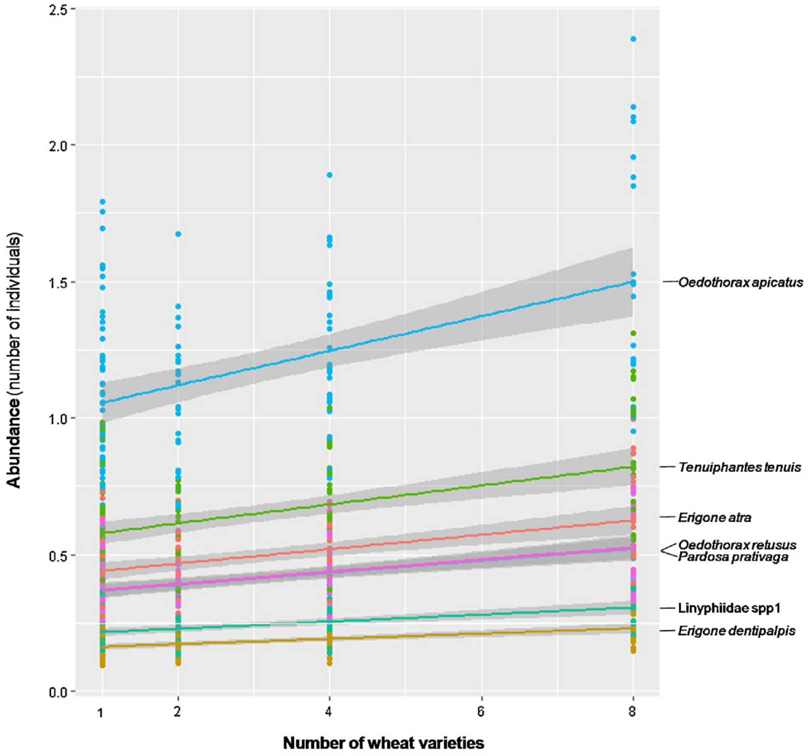

Fig. 3. Predicted abundance of spider species as a function of the number of wheat varieties. The dots and the lines are the values predicted by the generalized linear mixed-effect model including number of wheat varieties, latitude and longitude as explanatory variables.

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 Supplementary 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 Supplementary 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*) (Supplementary 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 Supplementary 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 Supplementary 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, Supplementary Appendix B: Fig. 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 Supplementary 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 Supplementary Appendix B: Table S3A).

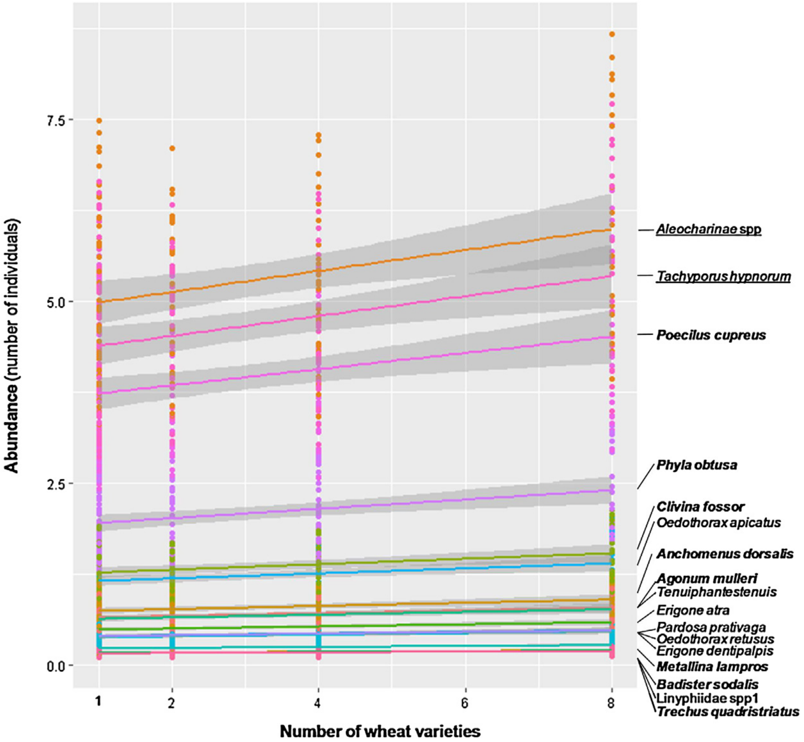

Fig. 4. Predicted abundance of predatory species as a function of the number of wheat varieties. Species names of ground beetles are in bold and rove beetles are underlined. Note that the spider species are the same as on Fig. 3, because all spiders are predators. The dots and the lines are the values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

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 Supplementary 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 Supplementary Appendix B: Table S3A) and predators as a whole ($\beta = 0.23 \pm 0.09$, $P = 0.012$, adjusted $R^2 = 0.05$, see Supplementary 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 Supplementary 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 Supplementary 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 Supplementary 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 (Fig. 1A and B). Longitude had also, in fewer cases, a significant but weak negative effect (see Supplementary 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 Supplementary 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 (Crutsinger et al. 2006; Chateil et al. 2013; 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 & Lauwton 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 Supplementary 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, Bohan, Shaw, & Weyman 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 (Hughes et al. 2008; Hersch-Green et al. 2011). Yet, few studies have successfully identified traits responsible for the effects of genotypic diversity (Crutsinger 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 m^2-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, Lajeunesse, & Agrawal 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.* Crutsinger et al. 2006; Moreira & Mooney 2013; Abdala-Roberts et al. 2016) 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 (±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 (Tscharntke 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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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.07.008.

References

Abdala-Roberts, L., Rasmann, S., Berny-Mier, Y., Tran, J. C., Covelo, F., Glauser, G., et al. (2016). Biotic and abiotic factors associated with altitudinal variation in plant traits and herbivory in a dominant oak species. *American Journal of Botany*, *103*, 2070–2078. http://dx.doi.org/10.3732/ajb.1600310

Andersen, A., Hansen, Å. G., Rydland, N., & ØYre, G. (1983). Carabidae and Staphylinidae (Col.) as predators of eggs of the turnip root fly *Delia floralis* Fallén (Diptera, Anthomyiidae) in cage experiments. *Journal of Applied Entomology*, *95*, 499–506. http://dx.doi.org/10.1111/j.1439-0418.1983.tb02673.x

Akritas, M. G. (1990). The rank-transformation method in some two-factor designs. *Journal of the American Statistical Association*, *85*, 73–78. http://dx.doi.org/10.1080/01621459.1990.10475308

Baret, F., de Solan, B., Lopez-Lozano, R., Ma, K., & Weiss, M. (2010). GAI estimates of row crops from downward looking digital photos taken perpendicular to rows at zenith angle: Theoretical considerations based on 3D architecture models and application to wheat crops. *Agricultural and Forest Meteorology*, *150*, 1393–1401. http://dx.doi.org/10.1016/j.agrformet.2010.04.011

Barot, S., Allard, V., Cantarel, A., Enjalbert, J., Gauffreteau, A., Goldringer, I., et al. (2017). Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. *Agronomy for Sustainable Development*, *37*, 13. http://dx.doi.org/10.1007/s13593-017-0418-x

Barton, K. (2017). *MuMIn: Multi-Model Inference. R package version 1.16.6.* https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. http://dx.doi.org/10.18637/jss.v067.i01

Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, *95*, 69–114. http://dx.doi.org/10.1079/BER2004350

Blandenier, G. (2009). Balloning of spiders (Araneae) in Switzerland; general results from an eleven-year survey. *Bulletin—British Arachnological Society*, *14*, 308–316. http://dx.doi.org/10.13156/arac.2009.14.7.308

Bohac, J. (1999). Staphylinid beetles as bioindicators. *Agriculture, Ecosystems and Environment*, *74*, 357–372. http://dx.doi.org/10.1016/S0167-8809(99)00043-2

Bohan, D. A., Boursault, A., Brooks, D. R., & Petit, S. (2011). National-scale regulation of the weed seedbank by carabid predators. *Journal of Applied Ecology*, *48*, 888–898. http://dx.doi.org/10.1111/j.1365.2011.02088.x

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135. http://dx.doi.org/10.1016/j.tree.2008.10.008

Bouthier, A., Pelosi, P., Villenave, C., Peres, G., Hedde, M., Ranjard, L., et al. (2014). Impact du travail du sol sur son fonctionnement biologique. In J. Labreuche, F. Laurent, & J. Roger-Estrade (Eds.), *Faut-il travailler le sol?* (pp. 85–108). Quae Editiors.

Brose, U. (2003). Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation structure or plant diversity? *Oecologia*, *135*, 407–413. http://dx.doi.org/10.1007/s00442-003-1222-7

Bryan, K. M., & Wratten, S. D. (1984). The responses of polyphagous predators to prey spatial heterogeneity — Aggregation by carabid and staphylinid beetles to their cereal aphid prey. *Ecological Entomology*, *9*, 251–259. http://dx.doi.org/10.1111/j.1365-2311.1984.tb00849.x

Cameron, A. C., & Trivedi, P. K. (1990). Regression-based tests for overdispersion in the Poisson model. *Journal of Economics*, *46*, 347–364. http://dx.doi.org/10.1016/0304-4076(90)90014-k

Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., et al. (2011). The functional role of producer diversity in ecosystems. *American Journal of Botany*, *98*, 572–592. http://dx.doi.org/10.3732/ajb.1000364

Chateil, C., Goldringer, I., Tarallo, L., Kerbiriou, C., Le Viol, I., Ponge, J.-F., et al. (2013). Crop genetic diversity benefits farmland biodiversity in cultivated fields. *Agriculture, Ecosystems and Environment*, *171*, 25–32. http://dx.doi.org/10.1016/j.agee.2013.03.004

Cook-Patton, S. C., McArt, S. H., Parachnowitsch, A. L., Thaler, J. S., & Agrawal, A. A. (2011). A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology*, *92*, 915–923. http://dx.doi.org/10.1890/10-0999.1

Crawford, K. M., & Rudgers, J. A. (2013). Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology*, *94*, 1025–1035. http://dx.doi.org/10.1890/12-1468.1

Crawley, M. J. (2009). *The R book*. Chicago: Wiley-Blackwell. http://dx.doi.org/10.1002/9781118448908

Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C., & Sanders, N. J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, *313*, 966–968. http://dx.doi.org/10.1126/science.1128326

Crutsinger, G. M. (2016). A community genetics perspective: Opportunities for the coming decade. *New Phytologist*, *210*, 65–70. http://dx.doi.org/10.1111/nph.13537

Eyre, M. (1994). Strategic explanations of carabid species distributions in northern England. In K. Desender, M. Dufrêne, M. Loreau, M. L. Luff, & J. P. Maelfait (Eds.), *Carabid beetles: Ecology and evolution. Series Entomologica* (Vol. 51) (pp. 267–275). Dordrecht: Springer. http://dx.doi.org/10.1007/978-94-017-0968-2_41

Finckh, M., Gacek, E., Goyeau, H., Lannou, C., Merz, U., Mundt, C., et al. (2000). Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agron*, *20*, 813–837. http://dx.doi.org/10.1051/agro:2000177

Freude, H. K., Harde, W., & Lohse, G. A. (1964). *Die Käfer Mitteleuropas. Band4. Staphylinidae I (Micropeplinae bis Tachyporinae)*. Krefeld: Goecke & Evers Verlag.

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., et al. (2012). AD Model builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, *27*, 233–249. http://dx.doi.org/10.1080/10556788.2011.597854

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (second edition). Thousand Oaks, CA: Sage. http://socserv.socsci.mcmaster.ce/jfox/Books/Companion

Gaba, S., Lescourret, F., Boudsocq, S., Enjalbert, J., Hinsinger, P., Journet, E. P., et al. (2015). Multiple cropping systems as drivers for providing multiple ecosystem services: From concepts to design. *Agronomy for Sustainable Development*, *35*, 607–623. http://dx.doi.org/10.1007/s13593-014-0272-z

Gaba, S., Alignier, A., Aviron, S., Barot, S., Blouin, M., Hedde, M., et al. (2018). Ecology for sustainable and multifunctional agriculture. In S. Gaba, B. Smith, & E. Lichfouse (Eds.), *Sustainable agriculture reviews 28, ecology for agriculture* (pp. 1–46). Cham: Springer International Publishing. http://dx.doi.org/10.1007/978-3-319-90309-5_1

Gotelli, N. J., & Colwell, R. K. (2011). Estimating species richness. In A. E. Magurran, & B. J. McGill (Eds.), *Biological diversity: Frontiers in measurement and assessment* (pp. 39–54). Oxford: Oxford University Press.

Hajjar, R., Jarvis, D. I., & Gemmill-Herren, B. (2008). The utility of crop genetic diversity in maintaining ecosystem services. *Agriculture, Ecosystems and Environment*, *123*, 261–270. http://dx.doi.org/10.1016/j.agee.2007.08.003

Harwood, J., Sunderland, K., & Symondson, W. (2001). Living where the food is: Web location by linyphiid spiders in relation to prey availability in winter wheat. *Journal of Applied Ecology*, *38*, 88–99. http://dx.doi.org/10.1046/j.1365-2664.2001.00572.x

Hatteland, B. A., Grutle, K., Mong, C. E., Skartveit, J., Symondson, W. O. C., & Solhoy, T. (2010). Predation by beetles (Carabidae, Staphylinidae) on eggs and juveniles of the Iberian slug *Arion lusitanicus* in the laboratory. *Bulletin of Entomological Research*, *100*, 559–567. http://dx.doi.org/10.1017/S0007485309990629

Hersch-Green, E. I., Turley, N. E., & Johnson, M. T. J. (2011). Community genetics: What have we accomplished and where should we be going? *Proceedings of the Royal Society B: Biological Sciences*, *366*, 1453–1460. http://dx.doi.org/10.1098/rstb.2010.0331

Hughes, A. R., Inouye, B. D., Johnson, M. T., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters*, *11*, 609–623. http://dx.doi.org/10.1111/j.1461-0248.2008.01179.x

Hůrka, K. (1996). *Carabidae of the Czech and Slovak Republics*. Ing. Vit Kabourek.

Johnson, M. T. J., Lajeunesse, M. J., & Agrawal, A. A. (2006). Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters*, *9*, 24–34. http://dx.doi.org/10.1111/j.1461-0248.2005.00833.x

Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, *3*, 157–164. http://dx.doi.org/10.2307/3235676

Kleiber, C., & Zeileis, A. (2008). *Applied econometrics with R*. New York: Springer-Verlag. https://CRAN.R-project.org/package=AER

Kremen, C., & Miles, A. (2012). Ecosystem services in biological diversified versus conventional farming systems: Benefits, externalities and trade-offs. *Ecol. Soc.*, *17*, 40. http://dx.doi.org/10.5751/ES-05035-170440

Kromp, B. (1999). Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment*, *74*, 187–228. http://dx.doi.org/10.1016/S0167-8809(99)00037-7

Lang, A. (2003). Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. *Oecologia*, *134*, 144–153. http://dx.doi.org/10.1007/s00442-002-1091-5

Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, *139*, 1–10. http://dx.doi.org/10.1007/s00442-004-1497-3

Larochelle, A. (1990). Food of carabid beetles. *Fabreries Supplement*, *5*.

Lefcheck, J. S. (2015). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology & Evolution*, *7*, 573–579. http://dx.doi.org/10.1111/2041-210X.12512

Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batary, P., Berendse, F., Bommarco, R., et al. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology Early View*, *23*, 4946–4957. http://dx.doi.org/10.1111/gcb.13714

Lobell, D. B., Schlenker, W., & Costa-Roberts, J. (2011). Climate trends and global crop production since 1980. *Science*, *333*, 616–620. http://dx.doi.org/10.1126/science.1204531

Loeuille, N., Barot, S., Georgelin, E., Kylafis, G., & Lavigne, C. (2013). Eco-evolutionary dynamics of agricultural networks: Implications for sustainable management. *Advances in Ecological Research*, *49*, 339–435. http://dx.doi.org/10.1016/B978-12-420002-9.00006-8

Loreau, M., & Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, *16*, 106–115. http://dx.doi.org/10.1111/ele.12073

Lott, D. A. (2009). The Staphylinidae (rove beetles) of Britain and Ireland: Scaphidiinae, Piestinae, Oxytelinae. Pt. 5. In *Handbooks for the identification of British insects*. Royal Entomological Society.

Lövei, G. L., & Sárospataki, M. (1990). Carabid beetles in agricultural fields in eastern Europe. In N. E. Stork (Ed.), *The role of ground beetles in ecological and environmental studies* (pp. 87–93). Andover, Hampshire: Intercept.

Mijatović, D., Van Oudenhoven, F., Eyzaguirre, P., & Hodgkin, T. (2013). The role of agricultural biodiversity in strengthening resilience to climate change: Towards an analytical framework. *International Journal of Agricultural Sustainability*, *11*, 95–107. http://dx.doi.org/10.1080/14735903.2012.691221

Moreira, X., & Mooney, K. A. (2013). Influence of plant genetic diversity on interactions between higher trophic levels. *Biology Letters*, *9*, 20130133 http://dx.doi.org/10.1098/rsbl.2013.0133

Nyfeler, D., Huguenin-Elie, O., Suter, M., Frossard, E., Connolly, J., & Lüscher, A. (2009). Strong mixture effects among four species in fertilized agricultural grassland led to persistent and consistent transgressive overyielding. *Journal of Applied Ecology*, *46*, 683–691. http://dx.doi.org/10.1111/j.1365-2664.2009.01653.x

Nyffeler, M., & Sunderland, K. D. (2003). Composition, abundance and pest control potential of spider communities in agroecosystems: A comparison of European and US studies. *Agriculture, Ecosystems and Environment*, *95*, 579–612. http://dx.doi.org/10.1016/S0167-8809(02)00181-0

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2016). *vegan: Community ecology package. R package version 2.4-1*. https://cran.r-project.org/web/packages/vegan/vegan.pdf

Parker, T. H., Forstmeier, W., Koricheva, J., Fidler, F., Hadfield, J. D., En Chee, Y., et al. (2016). Transparency in ecology and evolution: Real problems, real solutions. *Trends in Ecology & Evolution*, *31*, 711–719. http://dx.doi.org/10.1016/j.tree.2016;07.002

Peterson, B. G., Carl, P., Boudl, K., Bennett, R., Ulrich, J., Zivot, E., et al. (2014). *Performance analystics: Econometric tools for performance and risk analysis. R package version 1.4.3541*. https://cran.r-project.org/web/packages/PerformanceAnalytics/PerformanceAnalytics.pdf

Pfiffner, L., & Niggli, U. (1996). Effects of bio-dynamic, organic and conventional farming on ground beetles (Col. carabidae) and other epigaeic arthrods in winter wheat. *Biological Agriculture and Horticulture*, *12*, 353–364. http://dx.doi.org/10.1080/01448765.1996.9754758

Prieto, I., Violle, C., Barre, P., Durand, J. L., Ghesquiere, M., & Litrico, I. (2015). Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. *Nature Plants*, *1*, 15033. http://dx.doi.org/10.1038/nplants.2015.33

Ratnadass, A., Fernandes, P., Avelino, J., & Habib, R. (2012). Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: A review. *Agronomy for Sustainable Development*, *32*, 273–303. http://dx.doi.org/10.1007/s13593-011-0022-4

Roberts, M. J. (2001). *Spiders of Britain and Northern Europe*. London: Harper Collins.

Roger, J. L., Jambon, O., & Bouger, G. (2013). *Clé de détermination des Carabidaes Paysages agricoles du Nord-Ouest de la France*.

Scheu, S. (2002). The soil food web: Structure and perspectives. *European Journal of Soil Biology*, *38*, 11–20. http://dx.doi.org/10.1016/S1164-5563(01)01117-7

Schmidt, M. H., Clough, Y., Schulz, W., Westphalen, A., & Tscharntke, T. (2006). Capture efficiency and preservation attributes of different fluids in pitfall traps. *Journal of Arachnology*, *34*, 159–162. http://dx.doi.org/10.1636/T04-95.1

Shennan, C. (2008). Biotic interactions, ecological knowledge and agriculture. *Philosophical Transactions of the Royal Society B*, *363*, 717–739. http://dx.doi.org/10.1098/rstb.2007.2180

Siemann, E., Tilman, D., Haarstad, J., & Ritchie, M. (1998). Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*, *152*, 738–750. http://dx.doi.org/10.1086/286204

Skaug, H., Fournier, D., Bolker, B., Magnusson, A., & Nielsen, A. (2016). *Generalized linear mixed models using 'AD Model Builder'. R package version 0.8.3.3*.

Southwood, T. R. E., Brown, V. K., & Reader, P. M. (1979). The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society*, *12*, 327–348. http://dx.doi.org/10.1111/j.1095-8312.1979.tb00063.x

Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *American Naturalist*, *152*, 510–529. http://dx.doi.org/10.1086/286187

Symondson, W. O. C. (2004). Coleoptera (Carabidae, Staphylinidae, Lampyridae, Drilidae and Silphidae) as predators of terrestrial gastropods. In G. M. Barker (Ed.), *Natural enemies of terrestrial molluscs* (pp. 37–84). CABI Pub.

Terborgh, J. W. (2015). Toward a trophic theory of species diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 11415–11422. http://dx.doi.org/10.1073/pnas.1501070112

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., et al. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*, 79–92. http://dx.doi.org/10.1046/j.0305-0270.2003.0994.x

Thomas, D. B. (2008). Nontoxic antifreeze for insect traps. *Entomological News*, *119*, 361–365. http://dx.doi.org/10.3157/0013-872X-119.4.361

Tilman, D., & Downing, J. A. (1996). Biodiversity and stability in grasslands. *Nature*, *367*, 363–365. http://dx.doi.org/10.1038/367363a0

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., et al. (2001). Forecasting agriculturally driven global environmental change. *Science*, *292*, 281–284. http://dx.doi.org/10.1126/science.1057544

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., et al. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, *43*, 294–309. http://dx.doi.org/10.1016/j.biocontrol.2007.08.006

Vergnes, A., Pellissier, V., Lemperiere, G., Rollard, C., & Clergeau, P. (2014). Urban densification causes the decline of ground-dwelling arthropods. *Biodiversity and Conservation*, *23*, 1859–1877. http://dx.doi.org/10.1007/s10531-014-0689-3

Yee, D. A., & Juliano, S. A. (2007). Abundance matters: a field experiment testing the more individuals hypothesis for richness–productivity relationships. *Oecologia*, *153*, 153–162. http://dx.doi.org/10.1007/s00442-007-0707-1

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology & Evolution*, *1*, 3–14. http://dx.doi.org/10.1111/j.2041-210X.;1;2009.00001

Zuur, A. F., Saveliev, A. A., & Ieno, E. N. (2012). *Zero inflated models and generalized linear mixed models with R*. Highland Statistics Ltd.