

LETTER

Combined effects of agrochemicals and ecosystem services on crop yield across Europe

Vesna Gagic,^{1,2*} 
 David Kleijn,^{3,4}  András Báldi,⁵
 Gergely Boros,⁵
 Helene Bracht Jørgensen,⁶
 Zoltán Elek,^{5,7}
 Michael P. D. Garratt,⁸
 G. Arjen de Groot,⁴
 Katarina Hedlund,⁶
 Anikó Kovács-Hostyánszki,⁵ 
 Lorenzo Marini,⁹ Emily Martin,¹⁰
 Ines Pevere,⁹ Simon G. Potts,⁸
 Sarah Redlich,¹⁰ Deepa Senapathi,⁸
 Ingolf Steffan-Dewenter,¹⁰
 Stanislaw Świtek,¹¹
 Henrik G. Smith,^{6,12}
 Viktória Takács,¹¹
 Piotr Tryjanowski,¹¹
 Wim H. van der Putten,^{13,14} 
 Stijn van Gils¹³ and
 Riccardo Bommarco¹

Abstract

Simultaneously enhancing ecosystem services provided by biodiversity below and above ground is recommended to reduce dependence on chemical pesticides and mineral fertilisers in agriculture. However, consequences for crop yield have been poorly evaluated. Above ground, increased landscape complexity is assumed to enhance biological pest control, whereas below ground, soil organic carbon is a proxy for several yield-supporting services. In a field experiment replicated in 114 fields across Europe, we found that fertilisation had the strongest positive effect on yield, but hindered simultaneous harnessing of below- and above-ground ecosystem services. We furthermore show that enhancing natural enemies and pest control through increasing landscape complexity can prove disappointing in fields with low soil services or in intensively cropped regions. Thus, understanding ecological interdependences between land use, ecosystem services and yield is necessary to promote more environmentally friendly farming by identifying situations where ecosystem services are maximised and agrochemical inputs can be reduced.

Keywords

Agricultural intensification, biological pest control, ecological intensification, fertilisers, insecticides, landscape complexity, soil organic carbon, yield loss.

Ecology Letters (2017) 20: 1427–1436

INTRODUCTION

Industrialised agriculture following the Green revolution has been able to feed a growing world population, but large-scale land-use conversion and excessive use of inputs have also taken a heavy toll on the environment (Foley *et al.* 2011). Furthermore, in the past half century, yields have ceased to increase or even declined by 38.8% across several major cereal-growing areas (Ray *et al.* 2012). Thus, there is an urgent need to find novel ways to sustain production while minimising negative impacts on the environment (Pretty 2008). One suggested approach to achieve this is through ecological intensification of agriculture where active management of yield-supporting ecosystem services generated by biodiversity reduces the need of external inputs to sustain yields (Bommarco *et al.* 2013; Pywell *et al.* 2015).

Ecological intensification relies on multiple ecosystem services provided by biodiversity above and below ground. Above ground, a number of naturally occurring predatory and parasitic arthropods provide biological pest control services, reduce outbreaks of herbivorous insect pests and secure harvests that would otherwise be lost (Losey & Vaughan 2006). These beneficial organisms are generally highly mobile and depend on resources in the landscape surrounding the crop field (Schellhorn *et al.* 2015). There is compelling evidence that the diversity and level of biological pest control performed by mobile organisms depend strongly on the landscape surrounding crop fields and are generally lower in intensively cropped landscapes with little semi-natural, less disturbed habitats (Chaplin-Kramer *et al.* 2011; Rusch *et al.* 2016). Below ground, a great number of services are generated by soil organisms (Bender *et al.* 2016). Soil organic carbon

¹Department of Ecology, Swedish University of Agricultural Sciences, SE-75007 Uppsala, Sweden

²CSIRO, GPO Box 2583, Brisbane, QLD 4001, Australia

³Wageningen University and Research, Plant Ecology and Nature Conservation Group, NL-6708 PB, Wageningen, The Netherlands

⁴Wageningen University and Research, Alterra, NL-6708 PB, Wageningen, The Netherlands

⁵MTA Centre for Ecological Research, Institute of Ecology and Botany, Lendület Ecosystem Services Research Group, Alkotmány u. 2-4, H-2163 Vácrátót, Hungary

⁶Department of Biology, Lund University, SE-223 62 Lund, Sweden

⁷MTA-ELTE-MTM Ecology Research Group, Eötvös Loránd University, Biological Institute, Pázmány Péter sétány 1/C, Budapest H-1117 Hungary

⁸Policy and Development, Centre for Agri-Environment Research, School of Agriculture, University of Reading, Reading RG6 6AR UK

⁹University of Padova, DAFNAE, viale dell'Università 16, 35020 Legnaro, Padova, Italy

¹⁰Department of Animal Ecology and Tropical Biology, University of Würzburg, Biocenter Am Hubland, 97074 Würzburg, Germany

¹¹Poznan University of Life Sciences, Institute of Zoology, Wojska Polskiego 78/C, Poznan 60-625 Poland

¹²Centre for Environmental and Climate Research (CEC), Lund University, Lund SE- 22362, Sweden

¹³Department of Terrestrial Ecology, Netherlands Institute of Ecology NIOO KNAW, NL-6700 AB, Wageningen, The Netherlands

¹⁴Wageningen University and Research, Laboratory of Nematology, NL-6700 ES, Wageningen, The Netherlands

*Correspondence: E-mail: vesna.gagic@csiro.au

(SOC) is closely linked to, and often used as a proxy for several below-ground ecosystem services (Brady *et al.* 2015). SOC feeds the diverse community of below-ground organisms that increase soil fertility through breakdown of soil organic matter (Ernst & Emmerling 2009) and it is correlated with the size, complexity and functioning of soil food webs (de Rutier *et al.* 2005; Barrios 2007).

When examining the magnitude of effects on yield, yield-supporting ecosystem services are generally analysed individually. Their contributions to yield are often considered to be additive (Seppelt *et al.* 2011), although below- and above-ground food webs and ecological processes are clearly linked (de Deyn & van der Putten 2005; Kostenko *et al.* 2012). This hinders our ability to accurately predict the combined, net effects of ecosystem services on yield and find the best options for ecological intensification. For instance, an enhanced abundance of soil invertebrates might increase alternative prey for generalist predators above ground (Halaj & Wise 2002; Bell *et al.* 2008; von Berg *et al.* 2010) and potentially increase pest control service (Scheu 2001). The evidence for the interplay between ecosystem services and their combined contribution to final crop yield has begun to emerge (Lundin *et al.* 2013; Bartomeus *et al.* 2015), but knowledge gaps remain large and there is especially a lack of information from large-scale field trials.

The difficulty to accurately predict crop yield became even more apparent with recent evidence that benefits of ecosystem services for crop yield are likely to be affected by agricultural management and external inputs (Boreux *et al.* 2013; Klein *et al.* 2015; St-Martin & Bommarco 2016; Tamburini *et al.* 2016). Mineral fertiliser and insecticide inputs affect crop yield through increased nutrient availability and decreased pest pressure, but these agrochemicals can also pre-empt service benefits (e.g. Marini *et al.* 2015). However, increased yield due to fertilisers can also increase crop residuals after harvest that further add SOC. Understanding whether ecosystem services can replace, complement or interact with one another and with anthropogenic inputs in affecting yield is crucial for guiding management to simultaneously maximise production and minimise negative impacts on the environment.

Here, we used structural equation modelling to learn about mechanisms by which agricultural intensification at local field (agrochemical inputs), landscape and regional scales (increase in arable land area) impact aphid pests, their natural enemies and crop yield. Within each of seven European regions, we selected seven to nine field pairs with contrasting SOC content and embedded in landscapes with varying complexity (proportion of arable land). We added regionally recommended rates of insecticides and mineral fertilisers in a full-factorial design within each field. First, we expected that the positive effects of local management on yield would be changed through indirect pathways that include service providing organisms. As key pathways we expected a positive effect of insecticides on yield by reducing aphid abundances and a negative effect by releasing aphids from control by natural enemies. Similarly, we expected SOC and fertilisation to positively affect: (1) yield by increasing nutrient availability, (2) aphids by increasing plant quality and (3) natural enemies by cascading effects of alternative prey availability. Next, we assessed the relative

importance of the bottom-up and top-down forces affecting aphid pests and crop yield. The relative importance of these counteracting processes is difficult to predict and we have no prior expectations. Finally, landscape simplification has been found to decrease abundances of natural enemies of pests (Chaplin-Kramer *et al.* 2011) and to modify the effects of local field management on natural enemies ('Intermediate landscape hypothesis', Tscharntke *et al.* 2012). For example, according to the Intermediate landscape hypothesis high SOC in a field can be expected to have larger positive effect on natural enemies in more simplified (but not cleared) landscapes. Thus, we expected the effects on arthropods of agricultural intensification across spatial scales to be non-additive. Our results show cascading, non-additive effects of agricultural intensification at different scales on yield, with a dominant control through mineral fertilisation. Our findings highlight the difficulty to simultaneously exploit the benefits of both below- and above-ground ecosystem services in the current mainstream agriculture. However, we demonstrate how better understanding of ecological interdependences between ecosystem services and land use at local and landscape scale and their combined effect on crop yield, can help maximise the ecosystem service benefits and minimise agrochemical input and environmental degradation.

MATERIAL AND METHODS

Experimental design

We performed a replicated experiment in seven countries across Europe (Germany, Hungary, Italy, Poland, Sweden, the Netherlands and the UK) in 2014. We selected conventional winter wheat fields within one region of *c.* 100 × 100 km in each country. The regions (one per country) were located along a gradient of agricultural intensity with percentage arable land in the regions ranging from 40 to 77% and average grain yield from 3.8 to 9.5 t/ha (Table S1 in Appendix S1). In each region, we selected between seven and nine field pairs resulting in a total of 114 fields. Paired fields were selected to have contrasting levels of SOC (see Fig. S1 in Appendix S1 for distribution of SOC within countries) based mainly on contrasting management history (e.g. different crop rotation, organic matter input) that was not confounded with organic vs. conventional farming (Table S2 in Appendix S2), or with environmental factors, such as soil characteristics (e.g. more or less peaty soils, difference in ground water level). We sampled soils to determine soil type (Table S1 and Fig. S1 in Appendix S2) and validate that SOC levels differed, and that pH did not differ by more than 0.5 within field pairs (Appendix S2 Text 1). The median distance within field pairs was 1.2 km. Crop cultivars were matched within field pairs where possible (see Table S1 in Appendix S1 for cultivars used). To validate that the relationship between SOC and yield was not confounded with the effect of cultivars (e.g. cultivar A grown only in high SOC fields), we correlated average yield and average SOC per cultivar and found no relationship (Pearson's correlation = -0.22, $P > 0.1$).

Field pairs within each region were chosen across a gradient in landscape complexity ('Lcrop', Fig. S2 in Appendix S1) calculated as the proportion of arable land within a 1-km radius

around each study field (Rusch *et al.* 2016). The proportion of arable land is a commonly used measure of landscape simplification/complexity and it is often correlated with the proportion of semi-natural area and habitat diversity in the landscapes (see Rusch *et al.* 2016 and references therein). This design allowed us to test for individual effects of SOC and landscape complexity that were not related (Pearson's correlation = -0.045 , $P > 0.1$, Fig. S1 in Appendix S1). The landscape gradient was as broad as possible to represent the full extent of variation found in each region. Proportion of arable land in the region ('Rcrop') had a tendency to be negatively correlated with the average regional yield per unit area (Pearson's correlation = -0.72 , $P = 0.066$), both acquired from publicly available regional statistics collected by National Statistical Offices. The mean Lcrop per region and Rcrop were not correlated (Pearson's correlation = 0.08 , $P > 0.1$).

The treatments consisted of fully crossed presence and absence of insecticides and mineral (inorganic) fertilisers, randomly assigned to four treatment plots of at least 12×14 m in size along one of the field edges and 10 m from the nearest field corner (Fig. S3 in Appendix S1). Field boundary characteristics were matched within pairs and balanced among landscapes (e.g. we avoided having only forested edges in the complex landscapes). Pyrethroid (broad spectrum) insecticides were applied once using backpack sprayers after the first visual arthropod counts irrespective of actual pest attack rates, except in the UK where insecticides were applied simultaneously with that of the farmers. Fertilisers were ammonium nitrate except in one case (urea in Italy). Insecticides and fertilisers were applied by project members, consistently in terms of type and amount within a country and according to the regionally recommended rates (Table S1 in Appendix S1). Farmers were allowed to use herbicides and fungicides in the treatment plots. Regions that used high amounts of inorganic fertilisers had lower percentage arable land in the region (Spearman's rank correlation between 'Rcrop' and mineral fertiliser amount 'Ftotal': -0.813 , $P < 0.001$). Mean 'Ftotal' and 'SOC' per country were not correlated.

Biological control of aphid pests

We measured biological control of cereal aphids using a cage experiment (Rusch *et al.* 2013) in treatment plots without insecticide application. Visits to each field and establishment of the experiment were aligned with crop growth stage, identified based on Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie (BBCH), a decimal code for the growth stages of plants based on Zadoks *et al.* (1974). Four aphid populations of *c.* 50–100 grain aphids (*Sitobion avenae*) were established and protected by fibre tents in each treatment plot at growth stage BBCH 40–50 (booting). After 5–10 days, two populations where the aphid infestation was the most successful were randomly assigned to the cage treatment or open control. Cages were plastic cylinders with 5×5 mm mesh size (30 cm diameter and 100 cm high) inserted into a metal or plastic barrier (25 cm high, 32 cm diameter). Barriers were dug 10 cm into the soil to prevent ground-dwelling predators from entering the cages. Aphid natural enemies were removed from the cages prior to cage establishment and pitfall traps

were placed inside the cage to remove any remaining ground-dwelling natural enemies. To prevent flying predators from accessing the cages, mesh cylinders were sprayed with sticky glue. Aphid populations were counted non-destructively on at least ten randomly selected tillers at cage establishment and after 5 days when the experiment ended. Inoculation of aphids was not successful in Hungary.

A biological pest control index was calculated as $1 - [\text{number of aphids per tiller in open control at the end of the experiment}/(\text{aphid growth rate in cage} \times \text{number of aphids per tiller in open control at beginning of the experiment})]$ (Rusch *et al.* 2013). This index ranges from 0 (no aphids predated) to 1 (100% aphids predated). When the biocontrol index was negative, or aphid growth in the cage was lower in comparison with the open control, values of zero were assigned as it indicates unsuccessful biological pest control (Rusch *et al.* 2013; Tamburini *et al.* 2016). Negative growth of aphids in some of the cages was considered to be due to the unsuccessful predator exclusion and therefore removed from the analyses.

Abundance of pests and flying predators and activity–density of ground-dwelling predators

We visually counted aphids, vegetation-dwelling predators [ladybirds (Coccinellidae, adults and larvae), hoverflies (Syrphidae, larvae), lacewings (Chrysopidae, larvae)], and parasitised aphids (mummies) on 50–100 randomly selected shoots per treatment plot three times during the season at stem elongation, booting and heading. We assessed abundance of aphids and flying predators per tiller and parasitism rates: mummies/(mummies + live aphids). To assess activity–density of ground-dwelling predators we placed one pitfall trap within each treatment plot at least 10 m from the field edge. The pitfall traps were polypropylene beakers of height 155 mm and diameter 95 mm filled with 200 mL propylene glycol solution (1/3 glycol, 2/3 water) and a drop of detergent to reduce surface tension. Pitfall traps were covered with roofs (*c.* 10 cm above each trap) to prevent flooding by rain. The pitfall traps were placed in the treatment plots at wheat flowering and opened for a period of 10 days after which the activity–density of major predators [carabid beetles (Carabidae), rove beetles (Staphylinidae) and wolf spiders (Lycosidae)] was determined.

Crop yield

From each fertilisation and insecticide treatment plot, 1 m^2 (4 randomly located subplots of 0.25 m^2) of wheat was hand harvested. Yield was calculated as grain dry weight per hectare (t/ha).

Statistical analyses

To assess direct and indirect effects of agricultural intensification at local, landscape and regional scales and ecosystem services on yield, we developed two structural equation models (SEM). First, in the 'biological control model' ($n = 163$), we aimed to explain the direct and indirect effects of agricultural

intensification at different scales on the pest and yield via natural enemies and biological control they provide (Figs 1 and 2). Second, in the ‘insecticide model’ ($n = 441$), we aimed to quantify the effect of the insecticide application on the arthropods and yield (Fig. 3). We developed these two separate SEMs because BCI was measured only in plots without insecticides.

We used individual mixed effects models within piecewise SEMs. The random structure included field identity within the pair (1 : 2), nested within field pair identity (1 : 9), nested within region (1 : 7). We compared the relative importance of predictors using standardised (scaled by mean and variance) path coefficients (Schielzeth 2010). We also report unscaled estimates (where SOC, Lcrop, Rcrop are centred by overall mean, Tables S1 and S3 in Appendix S3). Since the range in Lcrop and SOC varied among countries, we report models with these variables standardised within countries (van de Pol & Wright 2009), when the output differed from the reported estimates. Collinearity was low in all individual models, as indicated by variance inflation factor (VIF) below 3.5. The mixed effects model residuals were visually checked for normality, homoscedasticity and spatial auto-correlation (spline correlograms). When necessary, we used variance functions (constant – ‘varIdent’ or exponential – ‘varExp’) to model heteroscedasticity and log transformation of the endogenous variables (all except for BCI) to model normality of residuals. We used partial correlation plots to visualise relationships among variables and to check the adequacy of model fit. To reduce SEM complexity and balance it with our sample size, we simplified each individual mixed effects model by removing

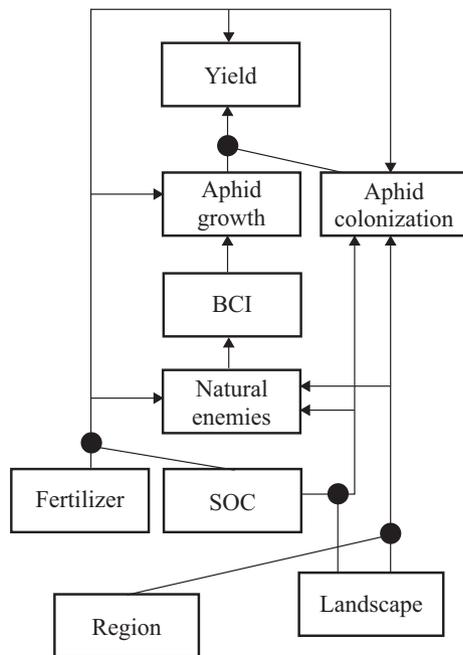


Figure 1 Initial casual diagram for biological control structural equation model (SEM). The diagram shows all tested relationships, including those that were tested in the preliminary analyses. The ‘natural enemies’ node represents the five natural enemy groups. The black circles show tested two-way interactions.

non-significant ($P < 0.05$) two-way interactions prior to including them in the SEMs. We used Akaike’s information criterion (AIC) and likelihood ratio test to compare models with and without interactions fitted with maximum likelihood estimation.

In the biological control model (Fig. 1), we expected that: (1) agricultural intensification at different scales will have direct effect on abundances of pests at colonisation time and abundances of their natural enemies with non-additive effect across spatial scales, (2) abundances of natural enemies will positively relate to the BCI, (3) BCI will reduce aphid growth, (4) yield will be reduced by aphid abundances expressed as an interaction between aphid colonisation (count 1) and growth (between counts 2 and 3). We did not include average aphid abundances across the second and the third counts in this model due to the inevitable spurious correlation with aphid growth. Hence, % SOC (continuous), fertilisation (two-level factor: 0, 1) and their interaction were predictors of yield, aphid growth and arthropod abundances. For arthropod abundances, additional predictors were percentage crop cover in the landscape (Lcrop) and region (Rcrop) and the two-way interactions between land use at different scales (Rcrop \times Lcrop and Lcrop \times SOC). For BCI, predictors were the five natural enemy groups. Aphid growth was additionally linked to BCI and crop yield to the interaction between aphid colonisation and growth. We assumed correlated errors among natural enemies of aphids.

In the insecticide model (Fig. 3a), we expected that: (1) insecticides (two-level factor: 0, 1) alone, or in interaction with SOC and fertilisers, would affect aphid abundances and their natural enemies, (2) natural enemies would negatively affect aphid abundances, (3) aphid abundances would reduce yield. Alternatively, we tested whether aphid abundances positively affect natural enemies in a separate SEM. Average aphid abundances were calculated using data from the counts 2 and 3 conducted after application of insecticides. Our preliminary analysis showed no main or interactive effect of insecticide on natural enemies of aphids and only two natural enemy groups related to aphids.

To assess the SEM model fit, we used directional separation test (D separation test) which yields Fisher’s C statistic that is chi-square distributed (Shipley 2009). If a model was rejected, connections were iteratively added until model acceptance was met and additional links interpreted as provisional discoveries of processes previously unanticipated (Grace 2006). We further simplified SEMs by removing the non-significant main effects. Alternative models were compared using AIC and changes in marginal R squares (Nakagawa & Schielzeth 2013). Additionally, we tested whether including percentage semi-natural vegetation instead of arable land changes the biological control model fit and interpretation.

To disentangle mechanisms, we separately tested whether there were any bottom-up effects of SOC, mineral fertilisation and their interaction on aphid growth within the enclosure cages. Aphid growth rate was calculated in all cases as: $[\log(\text{aphid number at time 2}) - \log(\text{aphid number at time 1})]$. We additionally analysed the ability of enhanced SOC to buffer yield decline in the short-term absence of mineral fertilisation (e.g. through nutrient retention and cycling). We calculated

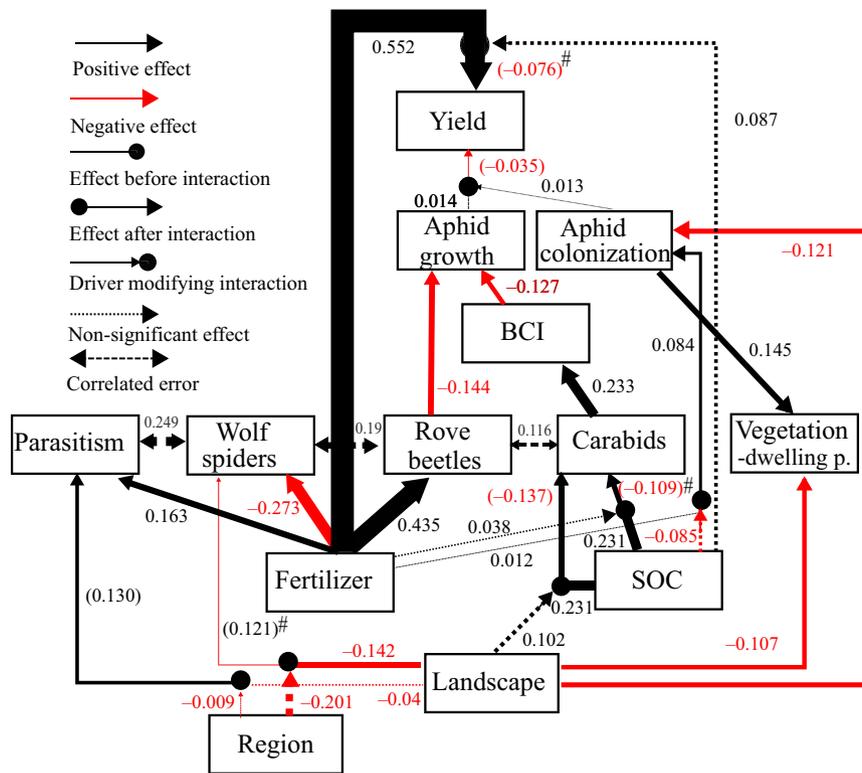


Figure 2 Biological control structural equation model (SEM) showing direct and indirect effects of soil organic carbon (SOC), fertilisation (presence/absence), landscape and regional simplification (calculated as percentage arable land) on aphids, their natural enemies, biological pest control (BCI) and yield. Thickness of paths is proportional to the given z -standardised path coefficients, including the adjusted effects after interactions for one of two variables. Non-significant paths are shown only when involved in a significant interaction. The numbers in parentheses show interaction coefficients. The hash symbol (#) marks interactions where significance differed with different standardisation methods (see Table S1 in Appendix S3). ‘Vegetation-dwelling p.’ is for vegetation-dwelling predators.

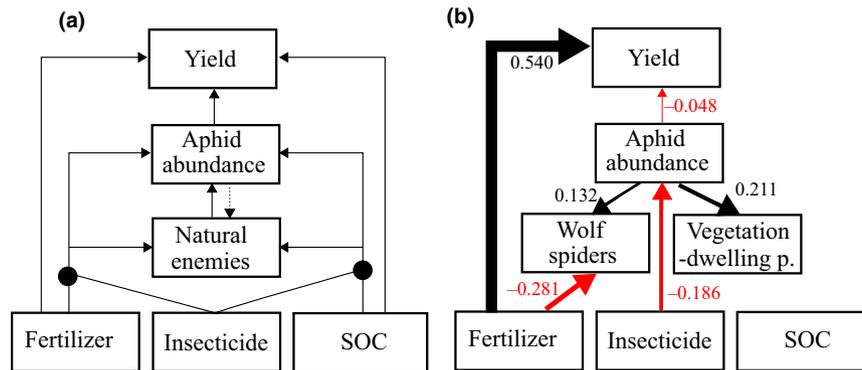


Figure 3 Insecticide structural equation model (SEM). (a) Initial casual diagram showing tested interactive effects of insecticides (presence/absence), soil organic carbon (SOC) and fertilisation (presence/absence) on aphids and their natural enemies and cascading effects on yield. The ‘natural enemies’ node represents the five natural enemy groups. The black circles show tested two-way interactions. The dotted arrow shows alternative model where aphid abundances were expected to positively affect natural enemies. (b) Best insecticide model thickness of paths is proportional to the given z -standardised path coefficients. ‘Vegetation-dwelling p.’ is for vegetation-dwelling predators.

the change in grain yield due to fertilisation as the log difference between yield in fertilised and in non-fertilised plots [$\log(\text{yield in fertilised plots}) - \log(\text{yield in unfertilised plots})$]. This index provides an estimate of the benefit of fertilisation treatment to yield, accounting for the variation in baseline non-fertilised yield, for example, due to regional intensity of cropping and previous fertiliser application rates (Table S1,

Fig. S4 in Appendix S1). We used a mixed effects model and related this index to SOC, amount of fertilisers applied (F_{total} , continuous variable ranging from 80 to 190 kg/ha), insecticide and their three-way interaction. Amount of fertiliser applied was included to account for an expected increasing in the yield difference in regions that applied more fertilisers. All analyses were performed in R version 3.2.0 (R Development

Core Team 2015) using packages ‘nlme’ (Pinheiro *et al.* 2015), ‘ncf’ (Bjornstad 2013), ‘Effects’ (Fox 2003), ‘visreg’ (Breheny & Burchett 2017) and ‘PiecewiseSEM’ (Lefcheck 2015).

RESULTS

The *a priori* biological control SEM showed poor fit (Fisher’s $C = 166.87$, $P = 0.009$). The D separation test revealed two missing links with significant path coefficients: (1) a negative link between rove beetles and aphid growth and (2) a positive link between aphid abundances at colonisation and vegetation-dwelling predator abundances (Fig. 2, Table S1 in Appendix S3). Including covariations between aphid abundances at colonisation and wolf spider activity–density, as well as between regional and landscape scale simplification and yield improved model fit, but the coefficients were not significant. The final biological control model (Fig. 2) represented our data well (Fisher’s $C = 141.8245$, $P = 0.07$; see also Table S2 in Appendix S3 for the marginal R^2). The insecticide SEM with the positive paths from aphid abundances to natural enemies had better fit (Fisher’s $C = 13.68$, $P = 0.474$, Fig. 3b) and was more biologically meaningful compared to the model with that path in the opposite direction (Fisher’s $C = 28.76$, $P = 0.004$).

Yield

Yields varied between 0.33 and 14.85 t/ha (median = 6.3). Fertilisation had the strongest positive effect on yield and increased yield by on average 32%. However, the effect of fertilisation on yield decreased with increased SOC, demonstrating decreased benefit of mineral fertiliser in fields with high SOC (Figs 2 and 4a). Aphids were weakly, but significantly related to yield. Aphid abundances alone (the insecticide model) and aphid growth coupled with high aphid colonisation (the biological control model) reduced yield.

Insecticide indirectly affected yield, wolf spiders and vegetation-dwelling predators by reducing aphid abundances by 44% (Fig. 3b and Table S3 in Appendix S3). We found no support for the indirect interactive effect of insecticide and SOC, or of insecticides and fertilisers on yield. However, we found a positive three-way interaction among SOC, insecticides and amount of fertilisers on the yield difference between fertilised and non-fertilised plots (Fig. 5 and Table S4 in Appendix S3).

Aphid pest

Aphid number per tiller varied between 0 and 10.6 (median = 0.14). For comparison, the economic injury level for the grain aphid in wheat in Sweden has been estimated to be 7 aphids per tiller. The biological control model revealed a top-down control of aphid growth in the field (Fig. 2). The importance of top-down control was further emphasised by a poor model fit when the link between BCI and aphid growth was omitted (Fisher’s $C = 148.42$, $P = 0.04$). We found no effect of SOC and fertilisation on aphid growth in the field, nor within the enclosure cages, indicating no bottom-up effect of plant quality on aphid growth in our experiment. Aphid

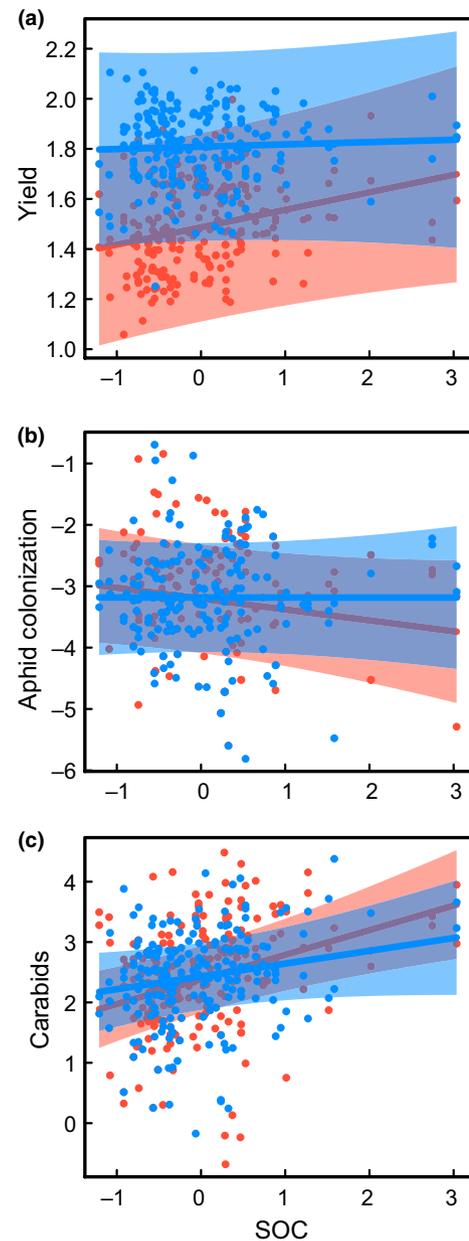


Figure 4 Partial residuals, prediction lines and confidence bands showing interactive effects of soil organic carbon (SOC) and fertilisation (presence in blue, absence in red) on log-transformed (a) yield, (b) aphid abundances at colonisation and (c) activity–density of carabid beetles.

colonisation was negatively affected by landscape simplification and positively by the interaction between SOC and fertilisers (Figs 2 and 4b).

Natural enemies of aphids and biological pest control

Carabid beetle activity–density was the only variable positively related to the BCI (Fig. 2). Carabid beetles were positively affected by SOC, but this effect was reduced in fertilised plots and in simplified landscapes (Figs 4c and 6, Table S1 in Appendix S3). The fertiliser treatment had positive effect on rove beetles and parasitism rates and negative on wolf spiders.

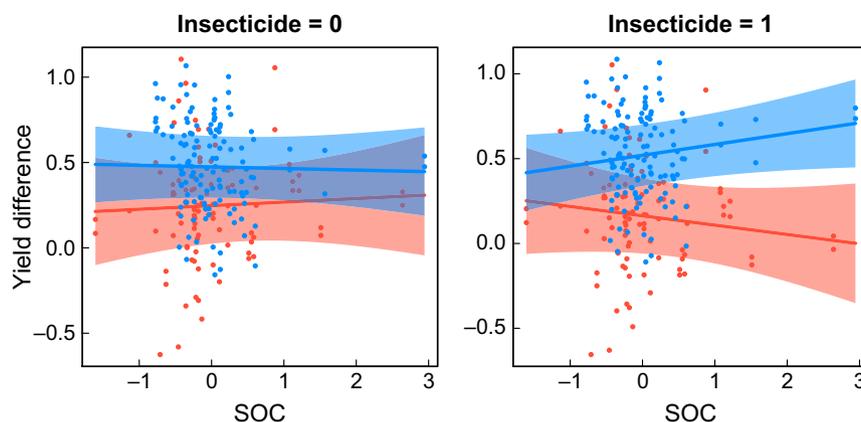


Figure 5 Partial residuals, prediction lines and confidence bands showing interactive effects of soil organic carbon (SOC) and fertilisation amount (90 kg/ha in red and 190 kg/ha in blue) on log yield difference between fertilised and unfertilised plots in the absence (left) and presence (right) of insecticides.

Landscape simplification had negative effect on vegetation-dwelling predators. The negative effect of landscape simplification on wolf spiders and parasitism rate was only evident in less intensively cropped regions (positive $L_{crop} \times R_{crop}$ interaction, Fig. S1 in Appendix S3). In separate models, we replaced R_{crop} with F_{total} to test whether the effects of regional simplification on natural enemies were confounded with fertilisation intensity, but found no effect of F_{total} .

Percentage semi-natural area was negatively correlated to percentage crop in the landscapes (Pearson's correlation = -0.42 , $P = 0.001$) and it was a worse predictor of aphid colonisation, carabids and parasitism rate and better predictor of wolf spiders in comparison to percentage crop. Here, we presented results for percentage crop as an indicator of landscape simplification (for the results with semi-natural area see Table S5 in Appendix S3).

DISCUSSION

Our results showed that field management and landscape simplification caused changes in pest and their natural enemy

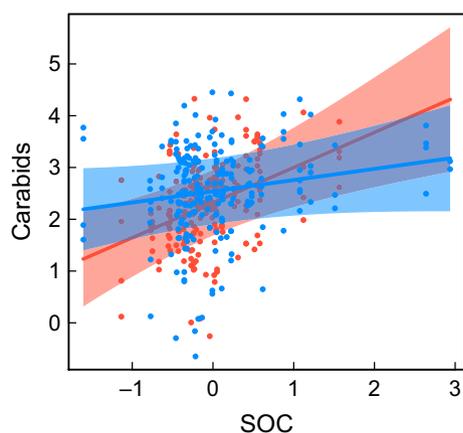


Figure 6 Partial residuals, prediction lines and confidence bands showing interactive effects of soil organic carbon (SOC) and landscape simplification (low = -11.8 in red and high = 13.6 in blue percentage arable land) on log-transformed activity-density of carabid beetles.

community with cascading effects on biological pest control and yield. Fertiliser application had dominant control over yield, both through direct and indirect effects and by altering the impact of SOC. The indirect effects on yield were smaller compared to direct effects due to significant, but weak, links between aphids and yield. Aphids were, in turn, affected by local field management directly (aphid colonisation) and indirectly through biocontrol (aphid growth). Furthermore, insecticides strongly reduced aphid abundances and thereby indirectly affected some natural enemies and yield.

These results demonstrate that SOC and biological pest control provide clear benefit to cereal yield, albeit weaker in comparison to fertilisation. The contribution of these ecosystem services must, however, be considered together with agrochemical inputs. Our field study confirms previous findings from plot experiments that SOC and mineral fertilisers do not additively benefit yield (Johnston *et al.* 2009; Brady *et al.* 2015). Countries with higher SOC levels benefited less from fertilisation, although they did not use fewer fertilisers. Furthermore, at high levels of SOC, mineral fertilisation decreased biological pest control by carabid beetles and increased aphid pest abundances at colonisation. Thus, mineral fertilisation decreased the benefit of both below- and above-ground ecosystem services to yield, while simultaneously increased aphid abundances.

The negative interactive effect of SOC and fertilisation on biological pest control and yield and a positive effect on aphids leads to the conclusion that the benefit of fertilisation and SOC to yield can be increased by insecticide spraying. This is because insecticides substantially reduced aphid abundances, but had no direct effect on their natural enemies. Indeed, we found that in the insecticide sprayed plots interactive effect of SOC and amount of fertilisation on the yield difference between fertilised and non-fertilised plots was positive (a three-way interaction). Thus, the yield benefit of fertilisation can vary depending on insecticide spraying and below- and above-ground ecosystem services. However, our experiment is likely to have underestimated the direct effects of insecticides on highly mobile natural enemies of pests because of diffusion from untreated areas (see also Macfadyen & Zalucki 2012).

Our data do not allow us to exactly determine which mechanisms are primary drivers of the observed results, and which mechanisms act secondarily. Optimal mineral balance in the plant promotes both plant growth and resistance to herbivores, but mineral fertilisers can shift this balance towards growth and reproduction, making the plant more palatable for herbivores ('The mineral balance hypothesis', Phelan *et al.* 1996). This can affect aphid colonisation and/or reproduction in the fields. We found no direct bottom-up effect of SOC and fertilisation on aphid growth in the fields or within predator enclosure cages. However, aphids were positively affected by fertilisation in high SOC fields through direct effects on aphid colonisation and indirect, top-down effects of biological pest control on aphid growth.

Biological pest control reduced aphid growth and was in turn positively related to carabid beetles. This does not mean that the other natural enemy groups were not important. More likely, other biodiversity indices, such as those that include functional traits of natural enemies would have been better predictors of BCI (Gagic *et al.* 2015). In addition, the structural equation model revealed a previously unanticipated direct link between rove beetles and aphid growth. This is likely due to the strong effect of rove beetles on aphid growth at low, but not at high aphid abundances as in our cage experiment. It should be noted that inherent problems in measuring biocontrol using cage experiment and open control call for caution when interpreting absolute values of BCI (Birkhofer *et al.* 2017).

Natural enemies of aphids were differently affected by SOC and fertilisers, presumably due to changes in prey community (Halaj & Wise 2002; Bell *et al.* 2008; von Berg *et al.* 2010). These results add to the evidence that nitrogen fertilisers can negatively affect aphid predator-prey ratio, but can also have a positive cascading effect on parasitoids (Zhao *et al.* 2015). Furthermore, the interactive effect of SOC and fertilisation on BCI through carabid beetles shows that increase in soil services also increases vulnerability of above-ground ecosystem services to local management. Supporting this, we found that biological pest control by carabid beetles tended to be additionally disrupted by landscape simplification in fields with high SOC. Thus, intensive land use at local and landscape scales hindered simultaneous harnessing of below- and above-ground ecosystem services.

At the landscape scale, our results for pest and vegetation-dwelling predators confirm previous findings that increasing percentage arable land negatively affects arthropods (Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011; Veres *et al.* 2013; Rusch *et al.* 2016). The lack of relationship between aphids, parasitoids and carabids and percentage semi-natural area indicate that the negative effects of percentage arable land on these arthropods are due to management practices, such as insecticide spraying in the surrounding fields, rather than to reduced availability of semi-natural habitats. Furthermore, the landscape effects on several natural enemies depended on land use at smaller (field) and larger (regional) scales, as expected. However, opposite to the 'intermediate landscape hypothesis', SOC had a tendency to benefit carabids more in complex landscapes presumably due to the dominance of agrobiont

species (well adapted to agriculture) in intensified fields, such as those with low SOC (Gagic *et al.* 2014). Furthermore, landscape complexity benefited wolf spiders and parasitoids the most in regions with a low proportion of agricultural land. Wolf spiders were virtually absent from intensively cropped regions where landscape complexity was not sufficient to increase their populations. Our low sample size at the regional level (seven) and correlation with other factors (e.g. fertilisation rate), warrants caution in interpreting results, but it highlights the importance of exploring land use at multiple spatial scales in relation to biological pest control. More generally, these results show that enhancing biological pest control through increasing landscape complexity may prove disappointing if regional context and local field management and related below-ground arthropod communities are not considered.

We conclude that when insecticides are applied together with fertilisers, yield can be maximised without consideration of ecosystem services that underpin yield. However, such intensified agricultural management is facing problems due to environmental degradation, development of pesticide resistance and worldwide failure to increase cereal yields in some regions (Pretty 2008; Foley *et al.* 2011; Ray *et al.* 2012). Our findings show that agroecosystem management that aims at reducing environmental degradation should consider combinations of multiple ecosystem services and multiple management inputs when developing strategies towards ecological intensification. This can allow us to reduce agrochemical inputs, alter the unwanted declines in some services and maximise their yield benefit. For example, it appears that insecticide spraying can be reduced in low SOC, fertilised or high SOC, unfertilised fields due to low pest abundances and high biological pest control in those fields. Contrary, in high SOC fertilised fields biocontrol was reduced, but can be maximised by increasing landscape complexity. Following this field-based proof of principle, the next challenge will be to determine how a transition can be made from current conventional input-driven farming to more sustainable, ecological-intensive farming while avoiding excessive yield losses in the longer term.

ACKNOWLEDGEMENTS

We thank four reviewers for their insightful comments on the manuscript and all the farmers across Europe for kindly letting us work on their lands. For technical assistance in the field and laboratory we thank Lorena Pumariño, Sophia Döös, Carol Högfeldt, Gerard Malsher, Dorottya Molnár, László Somay, Krisztina Bereczki, Jorge Martín Rodríguez, Ottó Szalkovszki, Matthias Jäger, Beate Wende, Rebecca Evans, Duncan Coston, Louise Truslove and Sara Ball. Funding was provided by the European Union to the FP7 project LIBERATION (grant 311781).

AUTHORSHIP

AB, RB, ZE, HBJ, MPDG, GAG, KH, AKH, DK, LM, EM, SGP, SR, ISD, VT, PT and SvG designed the study and

developed the sampling protocols. All authors contributed to performing the experiments, sampling and digitising the data. VG performed the analyses, and VG and RB interpreted results and wrote the manuscript. All authors contributed to the interpretation of results and writing.

REFERENCES

- Barrios, E. (2007). Soil biota, ecosystem services and land productivity. *Ecol. Econ.*, 4, 269–285.
- Bartomeus, I., Gagic, V. & Bommarco, R. (2015). Pollinators, pests and soil properties interactively shape oilseed rape yield. *Basic Appl. Ecol.*, 16, 737–745.
- Bell, J.R., Traugott, M., Sunderland, K.D., Skirvin, D.J., Mead, A., Kravar-Garde, L. *et al.* (2008). Beneficial links for the control of aphids: the effects of compost applications on predators and prey. *J. Appl. Ecol.*, 45, 1266–1273.
- Bender, S.F., Wagg, C. & van der Heijden, M.G.A. (2016). An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends Ecol. Evol.*, 31, 440–452.
- von Berg, K., Thies, C. & Tscharntke, T. (2010). Changes in herbivore control in arable fields by detrital subsidies depend on predator species and vary in space. *Oecologia*, 163, 1033–1042.
- Bianchi, F.J.J.A., Booij, C.J.H. & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes : a review on landscape composition, biodiversity and natural pest control. *Proc. Roy. Soc. Lond. B*, 273, 1715–1727.
- Birkhofer, K., Bylund, H., Dalin, P., Ferlian, O., Gagic, V., Hambäck, P.A. *et al.* (2017). *Methods to Identify the Prey of Invertebrate Predators in Terrestrial Field Studies*. Published online, *Ecol. Evol.*
- Bjornstad, O.N. (2013). ncf: spatial nonparametric covariance functions. R package version 1.1-5. Available at: <http://CRAN.R-project.org/package=ncf>. Last accessed 06.08.2017.
- Bommarco, R., Kleijn, D. & Potts, S.G. (2013). Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.*, 28, 230–238.
- Boreux, V., Kushalappa, C.G., Vaast, P. & Ghazoul, J. (2013). Interactive effects among ecosystem services and management practices on crop production: pollination in coffee agroforestry systems. *PNAS*, 110, 8387–8392.
- Brady, M.V., Hedlund, K., Cong, R., Hemerik, L., Hotes, S., Machado, S. *et al.* (2015). Valuing supporting soil ecosystem services in agriculture : a natural capital approach. *Agron. J.*, 107, 1809–1821.
- Breheny, P. & Burchett, W. (2017). visreg: Visualization of Regression Models. R package version 2.4-1. Available at: <https://CRAN.R-project.org/package=visreg>. Last accessed 06.08.2017.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.*, 14, 922–932.
- de Deyn, G.B. & van der Putten, W.H. (2005). Linking aboveground and belowground diversity. *Trends Ecol. Evol.*, 20, 625–633.
- Ernst, G. & Emmerling, C. (2009). Impact of five different tillage systems on soil organic carbon content and the density, biomass, and community composition of earthworms after a ten year period. *Eur. J. Soil Biol.*, 45, 247–251.
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M. *et al.* (2011). Solutions for a cultivated planet. *Nature*, 478, 337–342.
- Fox, J. (2003). Effect displays in R for generalised linear models. *J. Stat. Softw.*, 8, 1–27.
- Gagic, V., Haenke, S., Thies, C. & Tscharntke, T. (2014). Community variability in aphid parasitoids versus predators in response to agricultural intensification. *Insect Conserv. Divers.*, 7, 103–112.
- Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C. *et al.* (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proc. R. Soc. B*, 282, 20142620.
- Grace, J.B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press, New York.
- Halaj, J. & Wise, D.H. (2002). Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology*, 83, 3141–3151.
- Johnston, A.E., Poulton, P.R. & Coleman, K. (2009). Soil Organic Matter: its Importance in Sustainable Agriculture and Carbon Dioxide Fluxes. *Adv. Agron.*, 101, 1–57.
- Klein, A., Hendrix, S.D., Clough, Y., Scofield, A. & Kremen, C. (2015). Interacting effects of pollination, water and nutrients on fruit tree performance. *Plant Biol.*, 17, 201–208.
- Kostenko, O., van der Voorde, T.F.J., Mulder, P.P.J., van der Putten, W.H. & Bezemer, T.M. (2012). Legacy effects of aboveground – belowground interactions. *Ecol. Lett.*, 15, 813–821.
- Lefcheck, J.S. (2015). piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.*, 7, 573–579.
- Losey, J.E. & Vaughan, M. (2006). The economic value of ecological services provided by Insects. *Bioscience*, 56, 311–323.
- Lundin, O., Smith, H.G., Rundlof, M. & Bommarco, R. (2013). When ecosystem services interact: crop pollination benefits depend on the level of pest control. *Proc. R. Soc. Lond. B*, 280, 20122243.
- Macfadyen, S. & Zalucki, M.P. (2012). Assessing the short-term impact of an insecticide (Deltamethrin) on predator and herbivore abundance in soybean Glycine max using a replicated small-plot field experiment. *Insect Sci.*, 19, 112–120.
- Marini, L., Tamburini, G., Petrucco-Toffolo, E., Lindström, S.A.M., Zanetti, F., Mosca, G. *et al.* (2015). Crop management modifies the benefits of insect pollination in oilseed rape. *Agric. Ecosys. Environ.*, 207, 61–66.
- Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.
- Phelan, P.L., Norris, K.H. & Mason, J.F. (1996). Soil-management history and host preference by *Ostrinia nubilalis*: evidence for plant mineral balance mediating insect-plant interactions. *Environ. Entomol.*, 25, 1329–1336.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. & R Core Team (2015). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-120. Available at: <http://CRAN.R-project.org/package=nlme>. Last accessed date 06.08.2017.
- van de Pol, M. & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.*, 77, 753–758.
- Pretty, J. (2008). Agricultural sustainability : concepts, principles and evidence. *Philos. Trans. R. Soc. B*, 363, 447–465.
- Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M. *et al.* (2015). Wildlife friendly farming increases crop yield: evidence for ecological intensification. *Proc. R. Soc. Lond. B*, <https://doi.org/10.1098/rspb.2015.1740>.
- R version 3.2.0 (2015) – “Full of Ingredients” Copyright (C) 2015 The R Foundation for Statistical Computing. Vienna. ISBN 3-900051-07-0, <http://www.Rproject.org>
- Ray, D.K., Ramankutty, N., Mueller, N.D., West, P.C. & Foley, J.A. (2012). Recent patterns of crop yield growth and stagnation. *Nat. Commun.*, 3, 1293–1297.
- Rusch, A., Bommarco, R., Jonsson, M. & Smith, H.G. (2013). Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *J. Appl. Ecol.*, 50, 345–354.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D. *et al.* (2016). Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agric. Ecosys. Environ.*, 221, 198–204.
- de Rutier, P.C., Neutel, A.-M. & Moore, J. (2005). The balance between productivity and food web structure in soil ecosystems. In *Biological*

- Diversity and Function in Soils*. (eds Bardgett, R., Usher, M., Hopkins, D.). Cambridge University Press, Cambridge, pp. 139–153.
- Schellhorn, N.A., Gagic, V. & Bommarco, R. (2015). Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol. Evol.*, 30, 524–530.
- Scheu, S. (2001). Plants and generalist predators as links between the below-ground and above-ground system. *Basic Appl. Ecol.*, 2, 3–13.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.*, 1, 103–113.
- Seppelt, R., Dormann, C.F., Eppink, F.V., Lautenbach, S. & Schmidt, S. (2011). A quantitative review of ecosystem service studies: approaches, shortcomings and the road ahead. *J. Appl. Ecol.*, 48, 630–636.
- Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90, 363–368.
- St-Martin, A. & Bommarco, R. (2016). Soil compaction and insect pollination modify impacts of crop rotation on nitrogen fixation and yield. *Basic Appl. Ecol.*, 17, 1–10.
- Tamburini, G., Berti, A., Morari, F. & Marini, L. (2016). Degradation of soil fertility can cancel pollination benefits in sunflower. *Oecologia*, 180, 581–587.
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W. *et al.* (2011). The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecol. Appl.*, 21, 2187–2196.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P. *et al.* (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev. Camb. Philos. Soc.*, 87, 661–685.
- Veres, A., Petit, S., Conord, C. & Lavigne, C. (2013). Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agric. Ecosys. Environ.*, 166, 110–117.
- Zadoks, J.C., Chang, T.T. & Konzak, C.F. (1974). A decimal code for the growth stages of cereals. *Weed Res.*, 14, 415–421.
- Zhao, Z., Hui, C. & Li, B. (2015). Effects of agricultural intensification on ability of natural enemies to control aphids. *Sci. Rep.*, 5, 8024.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Christoph Scherber

Manuscript received 15 June 2017

First decision made 23 July 2017

Manuscript accepted 16 August 2017