Received: 11 May 2020 | Accepted: 7 December 2020

DOI: 10.1111/1365-2664.13821

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Sustainable landscape, soil and crop management practices enhance biodiversity and yield in conventional cereal systems

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Funding information
FP7 Project, Grant/Award Number: 311781

Handling Editor: Pieter De Frenne

Abstract

1. Input-driven, modern agriculture is commonly associated with large-scale threats to biodiversity, the disruption of ecosystem services and long-term risks to food security and human health. A switch to more sustainable yet highly productive farming practices seems unavoidable. However, an integrative evaluation of targeted management schemes at field and landscape scales is currently lacking. Furthermore, the often-disproportionate influence of soil conditions and agrochemicals on yields may mask the benefits of biodiversity-driven ecosystem services.
2. Here, we used a real-world ecosystem approach to identify sustainable management practices for enhanced functional biodiversity and yield on 28 temperate wheat fields. Using path analysis, we assessed direct and indirect links between soil, crop and landscape management with natural enemies and pests, as well as follow-on effects on yield quantity and quality. A paired-field design with a crossed insecticide-fertilizer experiment allowed us to control for the relative influence of soil characteristics and agrochemical inputs.
3. We demonstrate that biodiversity-enhancing management options such as reduced tillage, crop rotation diversity and small field size can enhance natural enemies without relying on agrochemical inputs. Similarly, we show that in this system controlling pests and weeds by agrochemical means is less relevant than expected for final crop productivity.
4. *Synthesis and applications*. Our study highlights soil, crop and landscape management practices that can enhance beneficial biodiversity while reducing agrochemical usage and negative environmental impacts of conventional agriculture. The diversification of cropping systems and conservation tillage are practical measures most farmers can implement without productivity losses. Combining local measures with improved landscape management may also strengthen the sustainability and resilience of cropping systems in light of future global change.

KEYWORDS

crop management, ecological intensification, landscape heterogeneity, natural enemies, pests, soil characteristics, sustainable intensification, wheat yield

1 | INTRODUCTION

Functional biodiversity generates essential ecosystem services to agriculture such as biological pest control, pollination and nutrient cycling. Yet, intensive agricultural practices threaten biodiversity and ecological functions thereby posing long-term risks to sustainable food production and human health (Dainese et al., 2019; Foley et al., 2005). A potential solution is the ecological intensification of farming, which allows farmers to enhance agricultural sustainability by managing biodiversity and yield-supporting ecosystem services via the reduction of intensive management practices (Bommarco et al., 2013; Pywell et al., 2015). But which practices are suitable for this purpose and what is their relative effect on yield compared to conventional, intensive methods?

Productivity of the staple crop winter wheat *Triticum aestivum* (L.) directly depends on agrochemical inputs, as well as soil characteristics, crop management, herbivory by pests, weed pressure and infections with pathogenic fungi (Ray et al., 2012). Degradation of soil fertility (Edmeades, 2003), inappropriate sowing densities (Ozturk et al., 2006) and herbivory (Dedryver et al., 2010) increase the gap between potential and attained yield in intensive wheat farming systems. Accordingly, management for healthy soils and crop diversification enhances the fertility and nutritional balance of the soil and improves productivity (McLaughlin & Mineau, 1995; Ratnadass et al., 2012). Similarly, soil, crop and landscape management that favours beneficial biodiversity (e.g. predators) and their top-down control on herbivorous pests (hereafter 'pests') may indirectly improve yield. This was shown for fertile soils (Birkhofer et al., 2008; Tamburini et al., 2016), reduced pesticide applications (Jonsson et al., 2012; Krauss et al., 2011) and fields located in diverse, well-connected cropping systems and landscapes (Fahrig et al., 2015; Martin et al., 2019; Redlich, Martin, Steffan-Dewenter, 2018).

However, responses to landscape heterogeneity are often variable or taxon-specific (Karp et al., 2018), and management practices that enhance both pests and predators may not result in improved pest regulation and yield (Tscharntke et al., 2016). Soil, management and landscape factors may also interactively influence predators, pests and productivity (Lichtenberg et al., 2017). For instance, the benefits of high soil organic carbon content (SOC) and biological control for winter wheat yield across Europe were reduced by mineral fertilizer application (Gagic et al., 2017). These potential trade-offs lower the anticipated benefits of management measures and farmers' trust in implementing research in real farming systems.

Implementation can further be hampered if drivers of biodiversity and productivity are difficult to manipulate. Even though natural habitat is important for biodiversity, the extent of cropland can rarely be reduced in very intensive cropping regions such as Germany. Other factors such as SOC content depend on the soil type, ploughing frequency and crop rotation. From a practitioner's perspective, it is advantageous to link biodiversity and yield to adaptable landscape structures (e.g. field size) or actual management practices (e.g. crop rotation diversity).

In this study and in contrast to previous research (Gagic et al., 2017; Garratt et al., 2018), we identify sustainable management practices that directly or indirectly reduce pests while maintaining beneficial biodiversity and high yields in conventional wheat systems. We concurrently consider variation of non-adaptable drivers (e.g. soil characteristics) and commonly used intensive farming practices (e.g. agrochemical application). Thereby, we aim to bridge the gap between science and practice by increasing our knowledge of local and landscape-scale management options that can achieve ecological intensification (Kleijn et al., 2019). We furthermore pre-empt criticism by practitioners regarding the transferability of results from small-scale, controlled experiments to real agroecosystems.

Based on previous research and ecological theory, we expected to find (a) positive effects of agrochemical usage, beneficial soil characteristics (e.g. high SOC) and reduced pests, weeds or diseases on wheat yield. However, we also hypothesized that (b) extensive crop management practices improving soil structure and fertility may directly increase productivity and add to ecological intensification. We further assumed that (c) soil, crop and landscape management that increases the spatial or temporal habitat and resource availability for specific arthropods may indirectly influence wheat productivity, either negatively (enhanced pest pressure) or positively (enhanced predator abundance). We investigated these potential links and their relative importance using structural equation modelling (SEM). As relationships between trophic levels (predators–pests–wheat) can be either negative (top-down processes, i.e. herbivory and pest control) or positive (resource-driven, bottom-up processes, i.e. host and prey availability) we assessed both options (Vidal & Murphy, 2018).

2 | MATERIALS AND METHODS

2.1 | Study design

A total of fourteen pairs of conventional winter wheat fields (28 fields) were selected in 2014 near Würzburg/Germany (49°47′N, 9°57′E) along a landscape heterogeneity gradient defined by the % semi-natural habitat cover within a 1-km radius around fields (Figure 1a, detailed design in Appendix S1 in Supporting Information). Fields were paired according to contrasting soil organic carbon content SOC (Figure 1b). To avoid correlations of SOC with other variables, we took care to (a) pair fields with similar pH, soil texture and field margin quality; (b) include pairs with different management practices (e.g. till or no-till, mineral vs. organic fertilizer input); and (c) minimize correlations between semi-natural habitat and other configurational and compositional landscape variables used in the analysis (Appendix S1). Average distance (mean ± *SD*) within and between field pairs was 1.07 ± 0.9 and 11.2 ± 3.8 km.

In each field, a randomized, fully crossed experiment with pyrethroid insecticide and mineral fertilizer was implemented in four adjacent treatment plots (12 × 14 m each, total 4 × 28 = 112 plots, Figure 1b). For both treatments, the type and amount of substance and the timing of application followed regional practices and recommendations (Figure 1c; Appendix S1). Fertilizer (total 190 kg/ha) was applied at three growth stages and compared well to fertilization

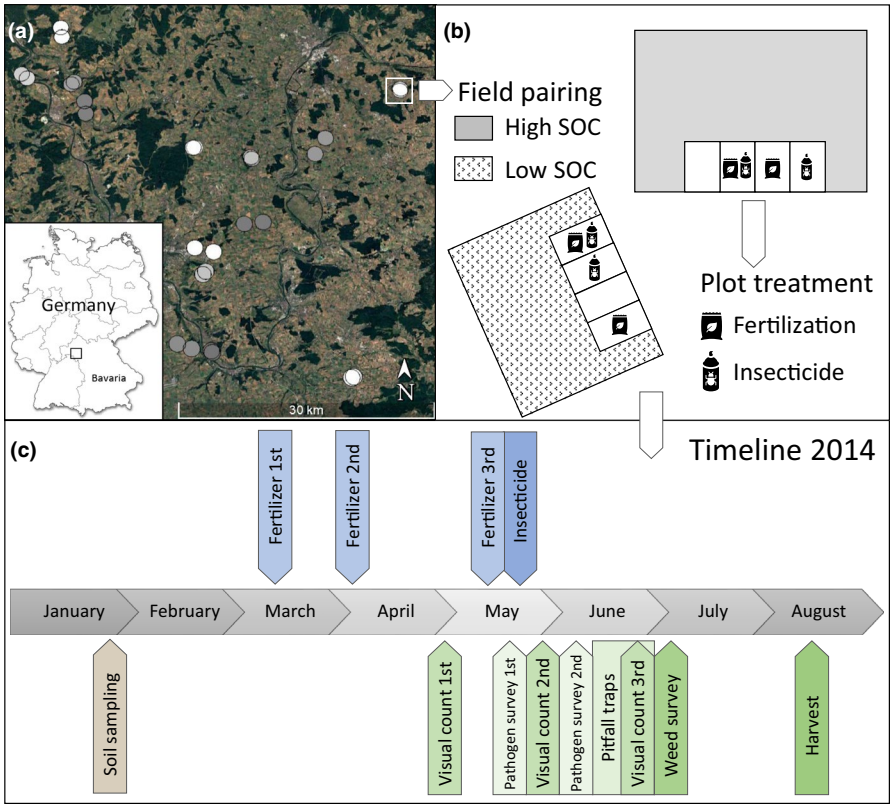


FIGURE 1 Experimental field set-up in winter wheat in Southern Germany (49°47′N, 9°57′E). Fourteen field pairs (grey circles, 1 km radii around fields) were selected along a landscape heterogeneity gradient (a). Each pair consisted of two fields with contrasting soil organic carbon content (high/low, b). In each field, a crossed fertilizer (yes/no, three applications) and insecticide (yes/no, one application) experiment was established (b). Treatment plots were used for assessment of biotic variables throughout the growing season (c) [Colour figure can be viewed at wileyonlinelibrary.com]

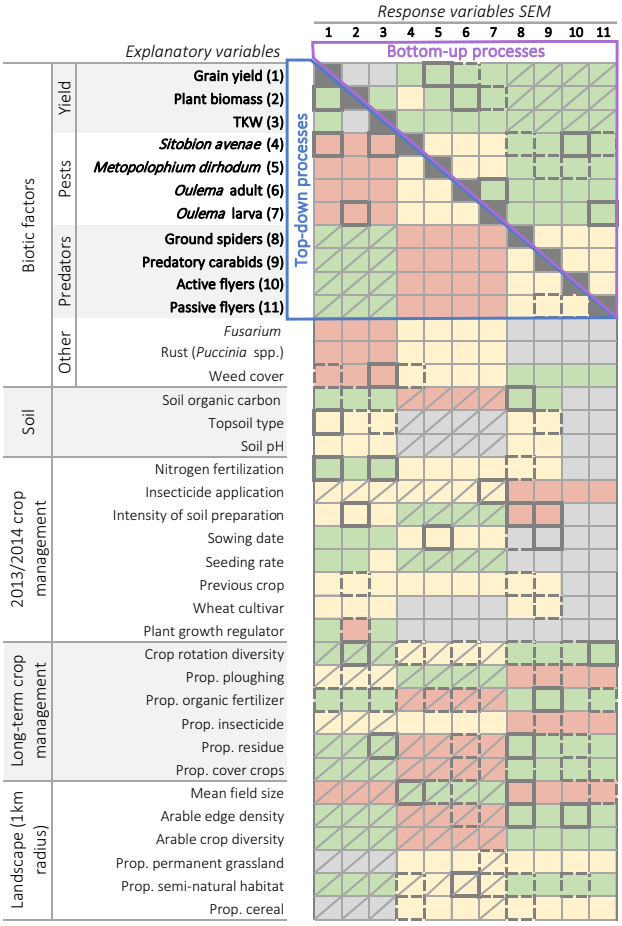
levels of surrounding conventional wheat fields (mean ± *SD* = 215.7 ± 42.8 kg/ha, range 120–339 kg/ha, farmer survey). Insecticide (active substance of beta-cyfluthrin, 300 ml/ha) was sprayed once after the first of three biodiversity surveys (Figure 1c) to test for temporal effects of insecticide application on pests and predators. In contrast to the integrated pest management framework of the Bavarian Regional Agricultural Institute, our study design required standardized insecticide application on all fields, even if pest thresholds were not crossed.

2.2 | Direct and indirect drivers of yield

We considered a total of 34 explanatory variables as potential direct or indirect drivers of wheat yield in our system. These can be separated into soil, crop management, landscape and biotic factors and were sampled at different spatial scales (Table 1; Appendix S1). The assessed soil characteristics likely to influence plant growth, yield, but also ground-dwelling predators (e.g. by providing suitable habitat conditions, Birkhofer et al., 2008) included SOC as proxy for soil organic matter, topsoil type and pH. We derived crop management data from the experimental set-up (fertilizer and insecticide treatment) and from farmer surveys performed in autumn 2014. The survey covered recent crop management in 2013/2014 and long-term management (mean ± *SD* data availability 11.25 ± 0.43 years), focussing on practices known or assumed to (in)directly affect pests, predators and yield. For instance, frequent no-till and organic fertilization should increase productivity but also ground-dwelling predators, as habitat is less disturbed and offers abundant alternative prey (Birkhofer et al., 2008). Similarly, we selected landscape heterogeneity variables in 1 km radius around study fields (ArcGIS v. 10.4, ESRI) including configuration and composition variables relevant for pests and their natural enemies. For example, landscapes with abundant semi-natural habitat cover or high crop diversity may enhance predators and pest regulation, thereby increasing productivity (Redlich, Martin, & Steffan-Dewenter, 2018).

The set of biotic variables that may directly (herbivory, disease) or indirectly (predation) determine yields comprised the abundance and activity density of pests and predators in our treatment plots. Responses to soil characteristics, management and landscape aspects and effects on productivity may be taxon-specific (Martin et al., 2019; Redlich, Martin, Wende, et al., 2018). We therefore divided arthropods into eight functional groups (four pest and four predator groups, Table 1). Within the pests, we differentiated between two main aphid species (Hemiptera: Sternorrhyncha), the English grain aphid *Sitobion avenae* (Fabricius), which preferentially occurs and feeds on the wheat grain thereby reducing grain yield, and the rose-grain aphid *Metopolophium dirhodum* (Walker), which feeds on stem and leaves and should influence plant biomass. Cereal leaf beetles *Oulema* spp. (Coleoptera: Chrysomelidae) were grouped as either larvae (sessile, cause leaf damage and potentially reduce plant biomass but not grain yield if compensation occurs) or adults (winged, mobile, responsive to landscape factors). Among predators, leaf-dwellers were classed as 'active flyers' (ladybirds [Coccinellidae, adults and larvae], hoverflies [Syrphidae, larvae], lacewings [Chrysopidae, larvae]) or 'passive flyers' (wind-dispersed

TABLE 1 Variables used in piecewise structural equation model (SEM). Grouping, description/methodology of variables and sampling scale with scale-specific means ± *SE* ('Plot' = variables in treatment plot, *n* = 112; 'Field' = variables in study fields, *n* = 28; 'Landscape' = variables in 1km radius around fields, *n* = 28). Each column labelled 1–11 represents a response variable (bold) of the SEM with hypothesized effects of 34 explanatory variables (effect colours: green = positive, red = negative, orange = positive or negative, grey = no hypothesis, diagonal line = expected indirect effect via trophic interactions). For trophic relationships among response variables, potential top-down effects are highlighted in the blue triangle, bottom-up effects in the purple triangle (only tested if trophic relationships were positive). Frames around hypothesized effects indicate (1) explanatory variables included in initial models but removed during simplification (grey dashed frames), (2) variables remaining in final models (significant terms, see Figure 2; continuous frames)



Scale	Mean ± SE	Variable description/methodology (more details in Appendix S1)
Plot	7.6 ± 0.24	Grain yield (t/ha), moisture-adjusted dry weight
Plot	8.2 ± 0.27	Plant biomass (t/ha) excluding grain, dry weight
Plot	44.03 ± 0.32	Thousand kernel weight (g), moisture-adjusted
Plot	143 ± 11.55	Summed aphid abundance (three surveys, Figure 1c)
Plot	7.17 ± 1.1	Summed aphid abundance (three surveys, Figure 1c)
Plot	1.98 ± 0.24	Summed cereal leaf beetle abundance (three surveys, Figure 1c)
Plot	7.32 ± 0.74	Summed cereal leaf beetle abundance (three surveys, Figure 1c)
Plot	3.72 ± 0.34	Activity density of ground-hunting spiders (10-day pitfall sampling, Figure 1c)
Plot	3.34 ± 0.38	Activity density of predatory carabid species (10-day pitfall sampling, Figure 1c)
Plot	1.78 ± 0.23	Summed abundance of flying predators dispersing as adults (three surveys, Figure 1c)
Plot	9.02 ± 0.58	Summed abundance of wind-dispersed leaf-dwelling spiders (three surveys, Figure 1c)
Plot	4.29 ± 0.7	Number of infested leaves (out of 50) at booting and flowering stage
Plot	5.51 ± 1.3	Number of infested leaves (out of 50) at booting and flowering stage
Plot	1.61 ± 0.5	% cover/m² of weedy forbs at fruit development stage
Field	1.39 ± 0.12	% SOC, mixed sample of five soil cores (3 cm Ø, 15 cm deep)
Field	Factor	Soil type based on soil maps ('loam', sandy 'clay' loam, 'sandy' loam)
Field	6.7 ± 0.06	pH of soil, mixed sample of five soil cores (3 cm Ø, 15 cm deep)
Plot	Factor	Fertilizer application on treatment plots ('yes', 'no')
Plot	Factor	Insecticide application on treatment plots ('yes', 'no')
Field	Factor	Low' (no-till), 'medium' (cultivator), 'high' (ploughing)
Field	291.5 ± 1.4	Julian date of winter wheat sowing
Field	191.7 ± 2.15	Seeding rate of winter wheat
Field	Factor	Crop preceding winter wheat in rotation
Field	Factor	Wheat cultivar grown
Field	Factor	Application of plant growth regulator ('yes', 'no')
Field	1 ± 0.05	Diversity of crop rotation
Field	0.5 ± 0.07	Frequency of intensive soil management (ploughing)
Field	0.34 ± 0.07	Frequency of organic fertilizer application
Field	0.23 ± 0.04	Frequency of insecticide application
Field	0.77 ± 0.05	Frequency residue remained on field
Field	0.16 ± 0.03	Frequency cover crop grown
Landscape	1.99 ± 0.18	Average patch size of arable fields (ha)
Landscape	126.35 ± 6.6	Density of crop – non-crop edges (m/ha)
Landscape	1.08 ± 0.04	Landscape-level crop diversity
Landscape	3.06 ± 0.79	Cover of managed permanent grassland (%)
Landscape	17.52 ± 1.97	Amount of semi-natural habitat including forest edges (%)
Landscape	54.4 ± 2.65	Proportion of cereal grown in landscape (%)

web-building spiders [Araneae]). While the first group is likely to benefit from large-scale landscape heterogeneity, the latter is thought to respond to field management. Abundances of all four pest and the two leaf-dwelling predator groups were counted on 50–100 tillers during three transect surveys (two after insecticide application, Figure 1c). Abundances per survey were then standardized to 50 tillers and summed across surveys to estimate pest pressure and pest control potential throughout the growing season (Table 1). For the two remaining soil-dwelling predator groups (ground beetles [Carabidae] and ground-hunting spiders [mainly Lycosidae]), we assessed activity density using pitfall traps (one sampling round after insecticide application; Table 1; Figure 1c). As additional biotic explanatory variables, we estimated weed pressure (% cover) of forbs in each treatment plot and infestation rates with the pathogenic fungi *Fusarium* and rust (*Puccinia* spp.). Pathogens were recorded in two visual surveys (Table 1; Figure 1c).

2.3 | Estimation of wheat yield

Compensation effects in response to pest or disease pressure are common in crops and can be identified by assessing different yield components. In every treatment plot, we measured three aspects of wheat productivity at harvest (Table 1; Figure 1c). Yield quantity was estimated as grain weight ('grain yield', t/ha) and plant biomass (t/ha). Both measures were extrapolated from four 0.25 m^{-2} subsamples. Thousand kernel weight (TKW, g) acted as proxy for yield quality. Yield components were treated as final response variables in our analysis (Table 1), but were also tested for correlations among each other.

2.4 | Statistical analysis

To quantify direct and indirect drivers of wheat productivity, we developed a piecewise *SEM*. The SEM consisted of eleven

individual path models with the response variables grain yield, plant biomass, TKW, *S. avenae*, *M. dirhodum*, *Oulema* larvae and *Oulema* adults, ground spiders, predatory carabids, active and passive flyers. As standardization of abundances and the nature of yield measures resulted in continuous, non-integer data, we implemented linear mixed effect models with Gaussian distributions. Abundances of pests and predators were log-transformed to improve normality of residuals. Explanatory variables for each model were pre-selected in three steps (details in Appendix S1). (a) Selection of 34 variables known or assumed to be of importance for response variables due to ecological theory (Table 1, coloured squares). (b) Sub-selection based on Pearson's correlation coefficients ($|r|>0.2|$, Table S1). The remaining explanatory variables were included in initial individual path models (Table 1, grey frames). (c) The resulting SEM was further simplified by removing non-significant terms ($p > 0.05$) using backwards elimination (dashed grey frames, Table 1; Table S2). Explanatory variables with marginal *p*-values ($p = 0.05–0.1$) or those initially excluded from models for lack of known ecological theory only entered individual models if their inclusion increased SEM fit based on AICc (mean field size influencing *S. avenae* abundance), or the directed separation test (D separation test, Shipley, 2009) revealed missing links with significant path coefficients (effects of sowing date on *M. dirhodum* and predatory carabids). For trophic relationships (predators–pests–wheat), we first assumed top-down, negative effects of enemies on pests and of pests on yield (Table 1, blue triangle). However, if positive, resource-driven correlations were observed (Table S1), we adapted the direction of links accordingly (Table 1, purple triangle).

As preliminary analyses did not reveal any interactive effects of soil characteristics and fertilisation regime on yield and soil-dwelling predators (Table S3), no interaction terms were included. A random intercept of 'Field' nested in 'Pair' accounted for multiple sampling within landscapes (field pairs) and fields (four treatment plots per field). Final individual path models (Table 1; Table S2) were validated graphically for normality, homoscedasticity and lack of spatial autocorrelation (Moran's *I*, $p > 0.802$). Collinearity in models was low (variance inflation factor < 3).

The final, simplified SEM showed good fit (*D* separation test, Fisher's $C = 356.2$, $p = 0.215$, Shipley, 2009) and conditional model fit (R^2) of individual path models ranged from 37% to 74% of variance explained (Figure 2). We assessed the relative importance of explanatory variables included in the final SEM using standardised path coefficients scaled by mean and variance (Schielzeth, 2010).

Additional mixed effects models tested for temporal insecticide effects on arthropods that may be masked in the SEM due to pooling of abundances across surveys. We fitted separate models for all pests and both groups of leaf-dwelling predators (no temporal sampling for soil-dwellers was conducted). Fixed terms were 'Survey' (three levels), insecticide application (yes/no) and their interaction. Although insecticide was only applied after the first biodiversity survey, all rounds were included to affirm the effectiveness of the pyrethroid application (i.e. that insecticide plots only showed lower aphid abundances after pesticide application). Post hoc Tukey multiple comparisons evaluated significant differences in arthropod abundances between surveys and insecticide treatments. A random intercept of 'Plot' nested in 'Field' nested in 'Pair' accounted for repeated sampling within landscapes, fields and treatment plots.

All analyses were performed in R version 3.3.2 (R Development Team, 2016) using packages NLME (Pinheiro et al., 2016), PIECEWISESEM (Lefcheck, 2016) , CAR (Fox & Weisberg, 2011) and VISREG (Breheny & Burchett, 2017).

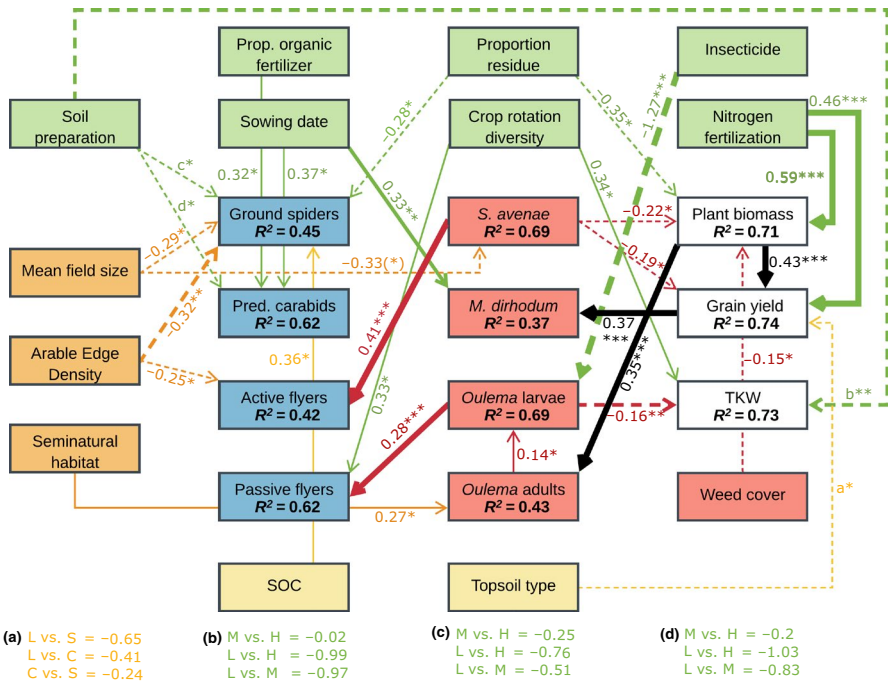


FIGURE 2 Path diagram of final structural equation model. Shown are direction (arrow), sign (negative = dashed line, positive = solid line) and strength (thickness of line) of relationships between landscape heterogeneity (orange), soil characteristics (yellow), crop management (green), natural enemies (blue), pests and weed (red) and yield components (white). The relative amount of explained variance (R^2) of individual path models, standardized path coefficients and their statistical significance ((*)$p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) are given. Letters and footnotes indicate effects and coefficients of the three-level factors soil type (L = loam, S = sandy, C = clay) and intensity of soil preparation (L = low, M = medium, H = high). TKW = Thousand kernel weight [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Direct effects on yield

Our average (±*SE*) grain yield (8.5 ± 0.3 t/ha) and TKW (44.2 ± 0.4 g) on fertilized plots compared well to mean yields in 2014 on the remaining area of our wheat fields (8.1 ± 0.3 t/ha, farmer surveys), in Germany (grain yield 8.6 t/ha, TKW ~ 44 g) and the neighbouring France, Europe's largest producer of wheat (grain yield 7.46 t/ha, TKW ~ 47 g). Plant biomass and grain yield were strongly correlated and increased with fertilizer application by 26% and 30% respectively (Figures 2 and 3a,d). Grain yield (not plant biomass) was significantly lower on soils with high sand content compared to loamy soil (−36%, Figures 2 and 3b,e). We found no direct links between yield and insecticide application, pH or SOC. The pest *S. avenae* had the strongest effect on yield quantity, with reductions being greater for biomass than grain yield (Figures 2 and 3c,f), yet *M. dirhodum* did not, as expected, reduce plant biomass. High densities of pest *Oulema* larvae resulted in lower TKW (Figure 2; Figure S1A), but not yield quantity. Neither the plant pathogen *Fusarium* nor rust had any effects on wheat yield, but weed cover reduced plant biomass and indirectly grain yield (indirect effect via biomass: −0.06, Figure 2).

Contrary to expectations, we did not observe any direct relationships between extensive crop management and yield quantity (grain yield and plant biomass). TKW, however, was larger on fields with high crop rotation diversity or no-till soil preparation (Figure 2; Figure S1B,C).

3.2 | Indirect effects on yield via herbivory

Of the 18 143 pest individuals recorded during three visual surveys, *S. avenae* was the most abundant species (89%), followed by *Oulema* larvae (5%), *M. dirhodum* (4%) and *Oulema* adults (2%). The main direct drivers of pest abundances were resource availability and agrochemical application. *Metopolophium dirhodum* and *Oulema* adults occurred in greater densities on plots with high grain yield or large plant biomass respectively (Figure 2; Figure S2B,C). Indirectly, both pests were therefore enhanced by nitrogen fertilization (indirect effects: 0.17 and 0.2 respectively). In contrast, insecticide application decreased *Oulema* larvae abundances by 78% (Figure 2; Figure S2D), with a positive follow-on effect on TKW (indirect effect: 0.2). No other pest showed a similar response to insecticide in models with pooled abundance used in the SEM. However, additional analyses using separate survey rounds revealed that—despite similar *S. avenae*

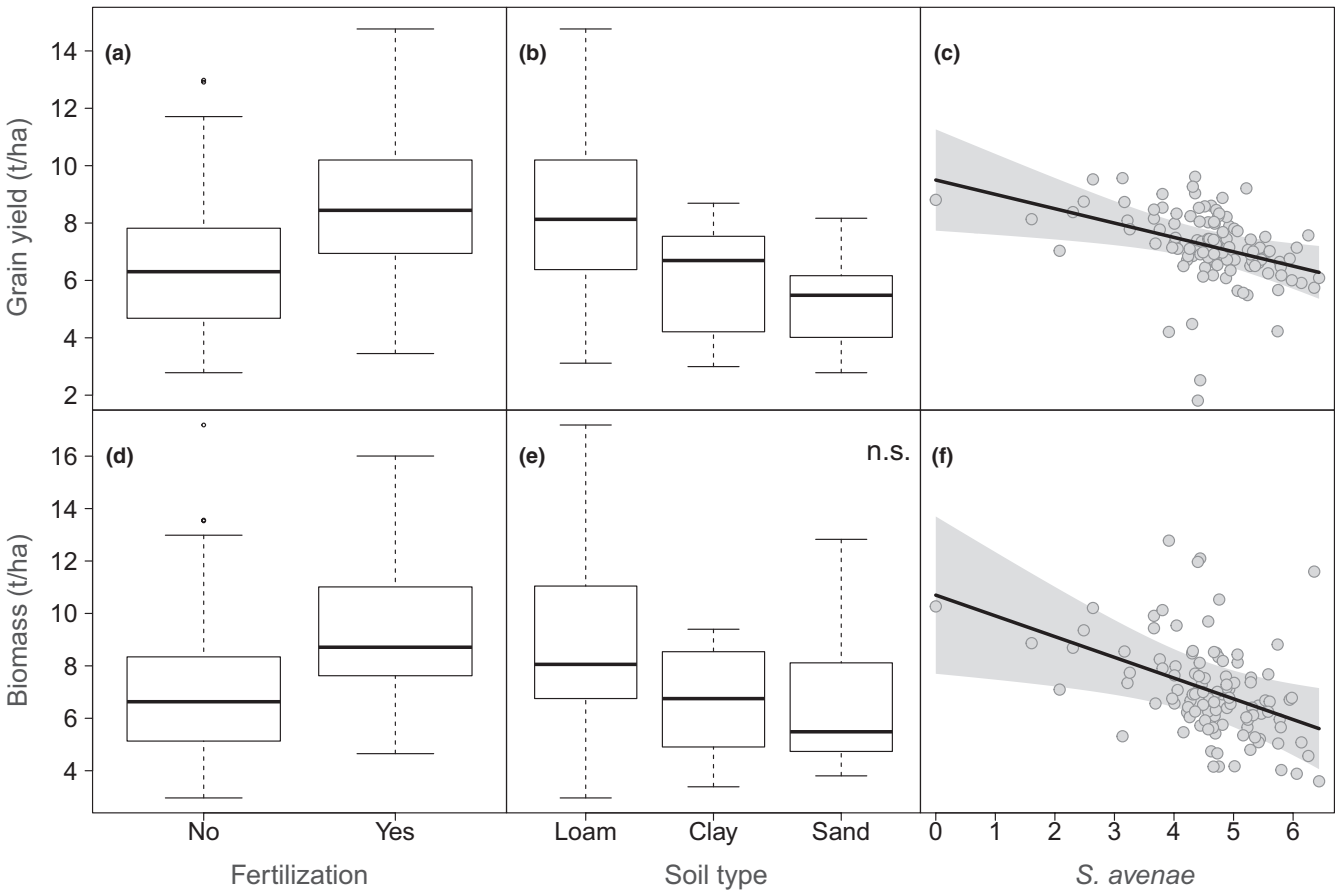


FIGURE 3 Main direct drivers of yield. Effects of fertilization, soil type and abundance of *Sitobion avenae* (log-transformed) on grain yield (t/ha, a–c) and plant biomass (t/ha, d–f). For continuous variables, partial residuals, prediction lines and 95% confidence bands are shown. 'n.s.' non-significant relationship

densities on all plots in survey 1—abundances in survey 2 were 60% lower on plots sprayed with pyrethroid directly beforehand compared to unsprayed plots. Still, aphid populations on insecticide plots quickly recovered (Tukey test comparing insecticide vs. non-insecticide plots, Survey 1: $p = 0.22$, Survey 2 (after insecticide application): $p < 0.001$, Survey 3: $p = 0.822$; Figure S3A). For *Oulema* larvae, this effect lasted longer (Survey 1: $p = 0.99$, Survey 2: $p < 0.001$, Survey 3: $p = 0.026$; Figure S3B). Unaffected by agrochemicals, the pest *M. dirhodum* showed positive responses to sowing date and was more prominent on fields sown later in the year (Figure 2; Figure S2E).

At the landscape scale, only two factors influenced pest populations (Figure 2). *Sitobion avenae* was less numerous in landscapes with large fields (Figure S2A), while *Oulema* adults—and to a lesser extent their offspring (indirect effect)—were enhanced by semi-natural habitat cover (Figure S2F,G). These correlations were rather weak though, as were the negative follow-on effects for yield quantity and quality respectively.

3.3 | Indirect effects on yield via predation

We recorded a total of 2,594 predators consisting of web-building spiders (48%), predatory carabids (30%), ground-hunting spiders (14%) and active flyers (8%, primarily Coccinellidae and Syrphidae). Of those, all leaf-dwelling predators responded positively to prey density, particularly to abundances of *S. avenae* (active flyers) and *Oulema* larvae (passive flyers; Figure 2; Figure S4B,C). Accordingly, insecticide-driven reductions of pest *Oulema* larvae indirectly affected passive flyers (indirect effect = −0.36). We did not, however, observe direct effects of insecticide on leaf-dwelling predators, neither using pooled abundances (SEM) nor distinct survey rounds (additional analyses). Temporal effects of insecticide application on soil-dwelling predators could not be tested, as pitfall traps were only opened once after insecticide application (Figure 1c; Table 1).

Instead, reduced soil disturbance, i.e. no-till as opposed to deep ploughing, increased ground-dwelling spiders and carabids by 32% and 49% respectively (Figures 2 and 4a,d). Furthermore, predatory carabids had higher activity densities in fields with frequent organic fertilizer application and late sowing of winter wheat (Figure 4e; Figure S4F). Densities of ground-hunting spiders increased with SOC content yet declined with the addition of plant residues (Figure 4b; Figure S4E). Leaf-dwelling predators were not affected by soil management, but crop rotation diversity enhanced the abundance of passive flyers (Figures 2 and 4f). Surprisingly, passive flyers were not affected by any other crop management factor.

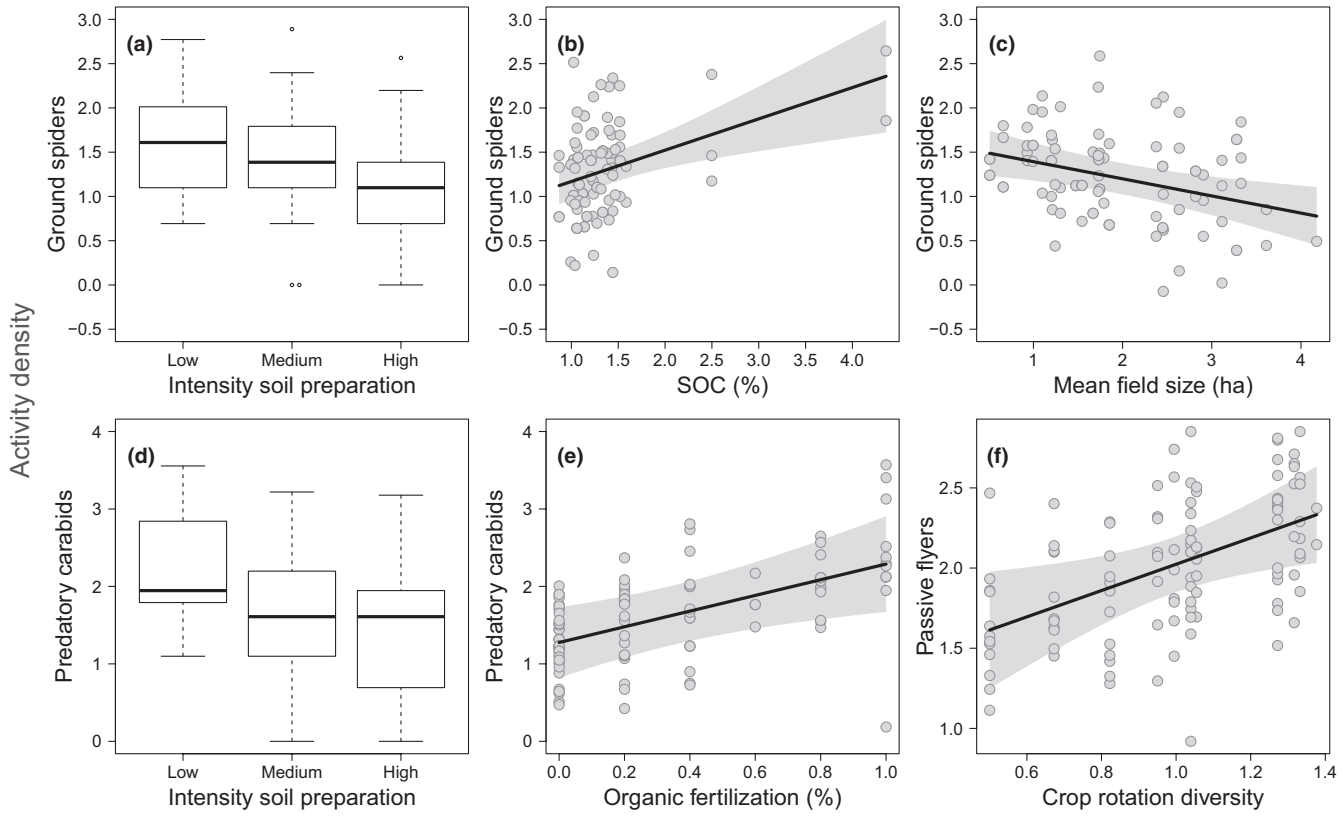


FIGURE 4 Direct effects of soil characteristics and crop management on natural enemies (log-transformed). Relationships between activity density of soil-dwelling predators and soil preparation intensity ('Low' = no-till, 'Medium' = surface cultivation, 'High' = deep ploughing, a, d), soil organic carbon content ('SOC', b), mean field size (ha, c) and frequency of organic fertilization in rotation (%, e). Influence of crop rotation diversity (Shannon–Wiener index) on passive flyers (wind-dispersed spiders, f). For continuous variables, partial residuals, prediction lines and 95% confidence bands are shown

In contrast to our predictions, landscape aspects at the scale assessed here played a minor role for predator abundances, with two exceptions. The activity density of ground-hunting spiders increased in landscapes with small crop fields (Figures 2 and 4c), yet decreased with high edge density (Figure S4D). Active (but not passive) flyers were less abundant in landscapes with high edge density (Figure S4A), which confirmed that active flyers respond more strongly to landscape than passive flyers. Still, we did not observe the expected positive response of active flyers to landscape heterogeneity.

We only observed positive relationships between predator and pest abundances, an indication for the prevalence of bottom-up, resource-driven processes in our system. Consequently, no beneficial indirect effects of predator abundances on yield were found.

4 | DISCUSSION

Input-driven, modern agriculture is commonly considered as basis for high crop production but also linked to ongoing health and environmental problems. Together with growing food demands, this calls for more sustainable farming systems able to maintain current levels of productivity. Ecological intensification (i.e. utilizing ecosystem services) aims to achieve this goal. In this study, we identify potential pathways for ecological intensification by investigating multifactorial direct and indirect drivers of yield in a real-world cereal agroecosystem. Although agrochemical inputs had the relatively strongest influence on yield quantity, our results indicate that reduced pesticide application may increase yield quality without causing additional pest pressure. We also demonstrate that biodiversity-enhancing management options such as no-till soil preparation and high crop rotation diversity can enhance natural enemies.

4.1 | Reduction of agrochemical use

In our study, ambiguous effects of fertilizer and insecticide highlight alternative options for maintaining yield quality and quantity under conditions of reduced agrochemical inputs. Even though grain yield and biomass were lower in non-fertilized plots, so was pest pressure ('plant vigour hypothesis', (Price, 1991)). This enhanced TKW, an important indicator of seeding vigour and milling quality of wheat. While insecticide decreased *Oulema* larvae, *S. avenae* as the most abundant and yield-damaging pest was not effectively controlled. Instead, *S. avenae* numbers quickly rebounded after short-term insecticide-driven reductions (Krauss et al., 2011). Accordingly, a reduction of fertilizer and insecticide in this system may benefit yield quality without significantly increasing pest pressure by *S. avenae*. An interesting finding, considering that insecticide and fertilizer treatments were applied following regional practices. However, although we used the typical application time, amount and substance, our experimental set-up required standardized insecticide applications independent of recommended thresholds defined by integrated pest management frameworks. On real farms, unnecessary, precautionary spraying may cause severe environmental damage and death of non-target species such as natural enemies. Even though we did not observe any negative effects of insecticide on leaf-dwelling predators, this could also be due to the specific type of insecticide used (pyrethroid) or rapid resettlement of relatively mobile web-building spiders and ladybirds from adjacent unsprayed plots.

4.2 | Enhanced soil fertility and structure

Although nitrogen tends to have the largest influence on productivity, soils with high carbon content (SOC) often augment yield (Gagic et al., 2017; Garratt et al., 2018). In our study region that was not the case, which could be explained by very low average SOC levels in Germany (mean ± *SE*: 1.39 ± 0.12%). However, we observed a positive influence of different soil management practices on yield and ground-dwelling predators. The enhanced condition and nutritional balance of diversely cropped, no-till soils provides optimal growing conditions for high quality crops, as illustrated here by TKW (McLaughlin & Mineau, 1995; Ratnadass et al., 2012). Furthermore, high soil organic matter content favours saprophagous insects such as springtails, which are important alternative prey for soil-dwelling predators. In contrast, ploughing alters physical characteristics of the soil and speeds decomposition of soil organic matter, causing unfavourable conditions for below-ground prey. Soil-dwelling predators therefore benefit from the combined effects of soil conservation practices (no-till, high crop diversity, addition of organic fertilizer, Bai et al., 2018).

4.3 | Ecological crop management

In addition to enhancing soil fertility and yield quality, diverse crop rotations are characterised by temporal resource diversity and reduced chemical inputs (McLaughlin & Mineau, 1995). This may explain the greater abundance of passive flyers (wind-dispersed spiders) on these fields. In addition, timely (as opposed to late) sowing of wheat allows for earlier crop maturation and can reduce pest pressure (Acreman & Dixon, 1985), as seen for *M. dirhodum*. Although numbers of predatory carabids were also lower on early sown fields, this response was less pronounced and could potentially be counteracted by no-till soil preparation.

4.4 | Diversifying the landscape

In contrast to soil and crop management, the role of landscape heterogeneity was small in our system. This could relate to limited coverage of the land use intensity gradients due to other constraints in site selection (e.g. contrasting SOC conditions) or the choice of spatial scale. The scale of landscape effects differs depending on the life history and movement capability of taxa (Chaplin-Kramer et al., 2011; Martin et al., 2016). In a previous multi-scale landscape study (Redlich,

Martin, & Steffan-Dewenter, 2018), we highlighted the advantages of landscape-level crop diversity at small and large scales, both for natural enemy abundances (<250 and >2,000 m scale) and biological control (<500 m scale). In other landscape studies, landscape composition or configuration at 1,000-m scales were the main drivers of biodiversity and ecosystem services (Bosem Baillod et al., 2017; Rusch et al., 2013; Tamburini et al., 2016). To avoid issues with multiple testing, we restricted the analysis of landscape effects in this study a priori to a well-supported intermediate spatial scale. While we may have missed some small or large-scale landscape effects, we nevertheless observed relevant relationships, with ground-dispersing spiders responding positively to small field sizes, but not to increased edge density. Predators in landscapes with small fields benefit from easy access to field boundary habitat and on-field prey (Fahrig et al., 2015). Yet a high density of crop-non crop boundaries may hinder their dispersal into fields if these structures act as barriers or provide competing resources (Ratnadass et al., 2012). Last, our monitoring efforts did not cover larger aerial predators like Vespid wasps that may have responded more readily to changes on the landscape scale.

In contrast to previous studies, pest densities did not decrease with landscape heterogeneity (Bianchi et al., 2006; Bosem Baillod et al., 2017) or host crop cover (Schneider et al., 2015). Instead, *Oulema* and *S. avenae* were more abundant in landscapes with large amounts of semi-natural habitat and smaller fields. Additional habitats and easy access to fields may therefore favour those pests in conventional agriculture. This calls for caution against proclaiming semi-natural habitat as a panacea of ecological intensification. Alternatively, heterogeneous landscapes may experience lower landscape-wide spraying intensities with less negative effects on pests, a possible correlation we could not test.

4.5 | Compensation potential

Our study shows that wheat can compensate for unfavourable soil conditions, weed competition and crop damage caused by pathogenic fungi or herbivory via changes to other yield components (Freeze & Bacon, 1990). For instance, crop damage by the plant pathogens rust and *Fusarium* (maximum infestation rate 58% and 34%, respectively), and feeding damage by *Oulema* larvae were very obvious on some fields. With the exception of TKW, however, our data did not confirm fears of participating farmers that this would lead to significant yield losses. In addition, yield reductions due to weed cover and *S. avenae* infestation had a greater negative influence on plant biomass than on grain yield. At the levels reached in our system, controlling these factors by agrochemical means is therefore less relevant than expected for final crop productivity.

4.6 | Linking biodiversity and pest control

Soil management and landscape aspects have the potential to enhance biodiversity, pest control services and consequently yield (Rusch et al., 2013; Tamburini et al., 2015). However, the negative relationships of the underlying top-down processes pest control and herbivory could not, or only partly, be confirmed. Instead, pests and predators primarily related to host and prey availability respectively. There are several explanations for this finding: (a) benefits of pest control are masked by effects of bottom-up resource availability and positive density dependence (Pywell et al., 2015; Vidal & Murphy, 2018). In this case, the only way to see benefits for biological pest control would have involved a predation experiment (e.g. predator exclusion). (b) Rather than natural enemy abundances, other trait-based functional biodiversity measures may have been a better indicator for pest control efficiency and yield (Gagic et al., 2015). (c) The importance of specific predator groups varies across the season. High initial densities of soil-dwelling predators at the beginning of the growing season are imperative for reducing initial pest infestations, while top-down control by this predator group may be lower or non-significant later on, as observed here (Birkhofer et al., 2008). (d) The recorded generalist predators are likely to have a more significant indirect effect on yield in other cropping systems that suffer from herbivory by chewing insects. In those cases, the management options identified here offer numerous possibilities for supporting pest control via ecological intensification.

5 | SYNTHESIS AND MANAGEMENT IMPLICATIONS

We combined a landscape gradient with a factorial field-scale experiment to identify practicable management options that can sustain biodiversity and winter wheat yield. Strengthening observed links between natural enemies and landscape (mean field size) or local management aspects (intensity of soil management, addition of soil organic matter, crop rotation diversity) may restore the pest control potential in this and other farming systems. These biodiversity-enhancing practices, together with expected benefits of agrochemical reductions and improved soil quality, provide important tools for ecological intensification. Accordingly, currently weak links between multiple ecosystem services and yield could be fostered by future adaptive soil, crop and landscape management and reduced agrochemical inputs. Considering the large-scale threats of conventional agriculture to biodiversity, the environment and human health, anticipated yet limited yield losses are an acceptable price relative to the economic and environmental benefits of a turnaround to more sustainable agriculture. In fact, we may even find that the strength of observed trophic relationships increases once legacy effects of long-term pesticide use fade away, further reducing potential yield gaps. Last, although this study is a snapshot of our system in time and results are closely linked to the climate in 2014, the observed effects of soil, management and landscape factors are likely to persist under different climatic conditions and may even be exaggerated due to climate change. These biodiversity-enhancing measures may strengthen the resilience of cropping systems to future global change drivers such as new pests and diseases or extreme weather events.

ACKNOWLEDGEMENTS

We thank the farmers for kindly permitting us to work on their land, and Matthias Jäger, Verena Seiffert and Florian Haydn for field and lab assistance. Crop and land use data were provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry and the Bavarian Surveying and Mapping Authority respectively. This study was performed within the FP7 Project LIBERATION ('LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificatION'), funded by the European Union, grant number: 311781. Open access funding enabled and organized by Projekt DEAL.

AUTHORS' CONTRIBUTIONS

E.A.M., S.R. and I.S.-D. conceived the idea and designed methodology; S.R. collected and analysed the field and survey data and led the writing of the manuscript. All authors interpreted the results, contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.bk3j9kd9m (Redlich et al., 2020).

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REFERENCES

Acreman, T. M., & Dixon, A. F. G. (1985). Developmental patterns in wheat and resistance to cereal aphids. *Crop Protection*, *4*(3), 322–328. https://doi.org/10.1016/0261-2194(85)90034-1

Bai, Z., Caspari, T., Gonzalez, M. R., Batjes, N. H., Mäder, P., Bünemann, E. K., de Goede, R., Brussaard, L., Xu, M., Ferreira, C. S. S., Reintam, E., Fan, H., Mihelič, R., Glavan, M., & Tóth, Z. (2018). Effects of agricultural management practices on soil quality: A review of long-term experiments for Europe and China. *Agriculture, Ecosystems & Environment*, *265*, 1–7. https://doi.org/10.1016/j.agee.2018.05.028

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. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*(1595), 1715–1727. https://doi.org/10.1098/rspb.2006.3530

Birkhofer, K., Bezemer, T. M., Bloem, J., Bonkowski, M., Christensen, S., Dubois, D., Ekelund, F., Fließbach, A., Gunst, L., Hedlund, K., Mäder, P., Mikola, J., Robin, C., Setälä, H., Tatin-Froux, F., Van der Putten, W. H., & Scheu, S. (2008). Long-term organic farming fosters below and aboveground biota: Implications for soil quality, biological control and productivity. *Soil Biology and Biochemistry*, *40*(9), 2297–2308. https://doi.org/10.1016/j.soilbio.2008.05.007

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*(4), 230–238. https://doi.org/10.1016/j.tree.2012.10.012

Bosem Baillod, A., Tscharntke, T., Clough, Y., & Batáry, P. (2017). Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *Journal of Applied Ecology*, *54*(6), 1804–1813. https://doi.org/10.1111/1365-2664.12910

Breheny, P., & Burchett, W. (2017). *visreg: Visualization of regression models*. R package version 2.3-0. Retrieved from https://CRAN.R-project.org/package=visreg

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. *Ecology Letters*, *14*(9), 922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *5*(10), eaax0121. https://doi.org/10.1126/sciadv.aax0121

Dedryver, C.-A., Le Ralec, A., & Fabre, F. (2010). The conflicting relationships between aphids and men: A review of aphid damage and control strategies. *Comptes Rendus Biologies*, *333*(6–7), 539–553. https://doi.org/10.1016/j.crvi.2010.03.009

Edmeades, D. C. (2003). The long-term effects of manures and fertilisers on soil productivity and quality: A review. *Nutrient Cycling in Agroecosystems*, *66*(2), 165–180. https://doi.org/10.1023/A:1023999816690

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K. F., Mitchell, S., & Tischendorf, L. (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, *200*, 219–234. https://doi.org/10.1016/j.agee.2014.11.018

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., & Snyder, P. K. (2005). Global consequences of land use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Sage. Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Freeze, D. M., & Bacon, R. K. (1990). Row-spacing and seeding-rate effects on wheat yields in the mid-south. *Journal of Production Agriculture*, *3*(3), 345–348. https://doi.org/10.2134/jpa1990.0345

Gagic, V., Hänke, S., Thies, C., & Tscharntke, T. (2015). Community variability in aphid parasitoids versus predators in response to agricultural intensification. *Insect Conservation and Diversity*, *7*(2), 103–112. https://doi.org/10.1111/icad.12037

Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H. B., Elek, Z., Garratt, M. P. D., de Groot, G. A., Hedlund, K., Kovács-Hostyánszki, A., Marini, L., Martin, E., Pevere, I., Potts, S. G., Redlich, S., Senapathi, D., Steffan-Dewenter, I., Świtek, S., Smith, H. G., … Bommarco, R. (2017). Combined effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecology Letters*, *20*, 1427–1436. https://doi.org/10.1111/ele.12850

Garratt, M. P. D., Bommarco, R., Kleijn, D., Martin, E., Mortimer, S. R., Redlich, S., Senapathi, D., Steffan-Dewenter, I., Świtek, S., Takács, V., van Gils, S., van der Putten, W. H., & Potts, S. G. (2018). Enhancing soil organic matter as a route to the ecological intensification of European arable systems. *Ecosystems*, *1–12*, https://doi.org/10.1007/s10021-018-0228-2

Jonsson, M., Buckley, H. L., Case, B. S., Wratten, S. D., Hale, R. J., & Didham, R. K. (2012). Agricultural intensification drives landscape-context effects on host–parasitoid interactions in agroecosystems. *Journal of Applied Ecology*, *49*(3), 706–714. https://doi.org/10.1111/j.1365-2664.2012.02130.x

Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A. E., Martínez-Salinas, A., O'Rourke, M. E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J. A., Schellhorn, N. A., Tscharntke, T., Wratten, S. D., Zhang, W., … Zou, Y. I. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(33), E7863. https://doi.org/10.1073/pnas.1800042115

Kleijn, D., Bommarco, R., Fijen, T. P. M., Garibaldi, L. A., Potts, S. G., & van der Putten, W. H. (2019). Ecological intensification: Bridging the gap between science and practice. *Trends in Ecology & Evolution*, *34*(2), 154–166. https://doi.org/10.1016/j.tree.2018.11.002

Krauss, J., Gallenberger, I., & Steffan-Dewenter, I. (2011). Decreased functional diversity and biological pest control in conventional compared to organic crop fields. *PLoS One*, *6*(5), e19502. https://doi.org/10.1371/journal.pone.0019502

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N. A., Carvalheiro, L. G., Snyder, W. E., Williams, N. M., Winfree, R., Klatt, B. K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., … Crowder, D. W. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology*, *23*(11), 4946–4957. https://doi.org/10.1111/gcb.13714

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., … Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, *22*(7), 1083–1094. https://doi.org/10.1111/ele.13265

Martin, E. A., Seo, B., Park, C.-R., Reineking, B., & Steffan-Dewenter, I. (2016). Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, *26*(2), 448–462. https://doi.org/10.1890/15-0856

McLaughlin, A., & Mineau, P. (1995). The impact of agricultural practices on biodiversity. *Agriculture, Ecosystems & Environment*, *55*(3), 201–212. https://doi.org/10.1016/0167-8809(95)00609-V

Ozturk, A., Caglar, O., & Bulut, S. (2006). Growth and yield response of facultative wheat to winter sowing, freezing sowing and spring sowing at different seeding rates. *Journal of Agronomy and Crop Science*, *192*(1), 10–16. https://doi.org/10.1111/j.1439-037X.2006.00187.x

Pinheiro, J., Bates, D., DebRoy, S., Deepayan, S., & R Development Team. (2016). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-128. Retrieved from http://CRAN.R-project.org/package=nlme

Price, P. W. (1991). The plant vigor hypothesis and herbivore attack. *Oikos*, *62*(2), 244–251. https://doi.org/10.2307/3545270

Pywell, R. F., Heard, M. S., Woodcock, B. A., Hinsley, S., Ridding, L., Nowakowski, M., & Bullock, J. M. (2015). Wildlife-friendly farming increases crop yield: Evidence for ecological intensification. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1816), 20151740. https://doi.org/10.1098/rspb.2015.1740

R Development Team. (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

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*(1), 273–303. https://doi.org/10.1007/s13593-011-0022-4

Ray, D. K., Ramankutty, N., Mueller, N. D., West, P. C., & Foley, J. A. (2012). Recent patterns of crop yield growth and stagnation. *Nature Communications*, *3*, 1293. https://doi.org/10.1038/ncomms2296

Redlich, S., Martin, E. A., & Steffan-Dewenter, I. (2018). Landscape-level crop diversity benefits biological pest control. *Journal of Applied Ecology*,*55*(5),2419–2428.https://doi.org/10.1111/1365-2664.13126

Redlich, S., Martin, E. A., & Steffan-Dewenter, I. (2020). Data from: Sustainable landscape, soil and crop management practices enhance biodiversity and yield in conventional cereal systems. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.bk3j9kd9m

Redlich, S., Martin, E. A., Wende, B., & Steffan-Dewenter, I. (2018). Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. *PLoS One*, *13*(8), e0200438. https://doi.org/10.1371/journal.pone.0200438

Rusch, A., Bommarco, R., Jonsson, M., Smith, H. G., & Ekbom, B. (2013). Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *Journal of Applied Ecology*, *50*(2), 345–354. https://doi.org/10.1111/1365-2664.12055

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schneider, G., Krauss, J., Riedinger, V., Holzschuh, A., & Steffan-Dewenter, I. (2015). Biological pest control and yields depend on spatial and temporal crop cover dynamics. *Journal of Applied Ecology*, *52*(5), 1283–1292. https://doi.org/10.1111/1365-2664.12471

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*(2), 363–368. https://doi.org/10.1890/08-1034.1

Tamburini, G., De Simone, S., Sigura, M., Boscutti, F., & Marini, L. (2015). Conservation tillage mitigates the negative effect of landscape simplification on biological control. *Journal of Applied Ecology*, *53*(1), 233–241. https://doi.org/10.1111/1365-2664.12544

Tamburini, G., Simone, S. D., Sigura, M., Boscutti, F., & Marini, L. (2016). Soil management shapes ecosystem service provision and trade-offs in agricultural landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1837), 20161369. https://doi.org/10.1098/rspb.2016.1369

Tscharntke, T., Karp, D. S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E. A., Martínez-Salinas, A., Meehan, T. D., O'Rourke, M., Poveda, K., Rosenheim, J. A., Rusch, A., Schellhorn, N., Wanger, T. C., … Zhang, W. (2016). When natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation*, *204*(Part B), 449–458. https://doi.org/10.1016/j.biocon.2016.10.001

Vidal, M. C., & Murphy, S. M. (2018). Bottom-up vs. top-down effects on terrestrial insect herbivores: A meta-analysis. *Ecology Letters*, *21*(1), 138–150. https://doi.org/10.1111/ele.12874

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Redlich S, Martin EA, Steffan-Dewenter I. Sustainable landscape, soil and crop management practices enhance biodiversity and yield in conventional cereal systems. *J Appl Ecol*. 2021;58:507–517. https://doi.org/10.1111/1365-2664.13821