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Redefining the field to mobilize three-dimensional diversity and ecosystem services on the arable farm

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ABSTRACT

In this article we explore the concept and implications of three-dimensional (spatial, temporal, and genetic) in-field crop diversification to inform systems redesign towards ecological intensification. We first present a conceptual framework for classifying diversity in arable contexts. We then apply the framework to analyse two long-term systems experiments in The Netherlands where spatial and genetic diversity measures were implemented via strip and mixed intercropping with the aim to increase ecosystem service delivery: incidence and spreading rate of late blight (*Phytophthora infestans*) in potato (*Solanum tuberosum* L.), and biocontrol control potential in wheat (*Triticum aestivum* L.). In the case of late blight, potatoes planted in strips had significantly lower disease incidence than the monoculture reference across all years, and adding cultivar mixing within the strip was more powerful in mitigating late blight than spatial diversification alone. In the case of biocontrol in wheat, strips supported significantly larger (for all but one taxonomic group) and significantly more diverse epigeic natural enemy populations than the sole culture reference in all years. However, the addition of species mixing within strips did not further increase biocontrol indices compared to sole-wheat strips. These results imply that compromises between management complexity and ecosystem service enhancement are achievable through strip cropping, an operable practice with current machinery, and one that does not require a thorough reconfiguration of the production system. The three-dimensional diversity framework proved useful for unpacking experimental outcomes in terms of diversity-mediated mechanisms, however it requires further development before it can be used to facilitate multi-objective optimization.

1. Introduction

In arable farming, the field is an important management unit which shapes how a farmer conceptualizes and executes cultivation activities. In Europe as in other parts of the world, the initiation of agricultural industrialization efforts post-WWII (in part supported by land reallocation and consolidation policies) led to a change in the size, composition, and configuration of arable fields as farms adapted to accommodate larger farm machinery, a drive to specialize, and the demands of new economies of scale (Jepsen et al., 2015). Over the last several decades, these adaptations have led to a general shift towards

larger arable fields, the domination of monocropping, and simplified agricultural landscapes (Eurostat, 2018; van der Zanden et al., 2016; van Vliet et al., 2015).

In combination with how a farmer manages it, field size, composition, and configuration dictate what effect arable farming has on the delivery of various ecosystem (dis)services (Fahrig et al., 2015; Sirami et al., 2019). A monocultural approach to arable agriculture enables farmers to treat entire fields, no matter how big, as a single unit of management where cultivation tasks may be executed with efficiency by large-scale machinery. However, large extents of genetically uniform plants rarely occur in nature, and maintaining them in agriculture

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requires heavy reliance on external inputs and control-driven management. While heralded as technological breakthroughs that helped reduce hunger worldwide (i.e. the Green Revolution), it is now known that widespread applications of synthetic fertilizers and crop protection products, together with concurrent agricultural landscape simplification, have contributed to a cascade of failing ecosystem controls and the overstepping of multiple planetary boundaries (Campbell et al., 2017; Kinzig et al., 2006).

In low-diversity arable systems that rely heavily on external inputs, crop production capacities are exploited at the cost of ecological processes which support and regulate natural systems (Foley et al., 2005; Haddad et al., 2015; Patzek, 2008; Tilman et al., 2011). A logical solution to restoring these processes would be to bring diversity back into the arable field, as lessons from ecology and agronomy show that diversification is a key ingredient in both productivity and the delivery of other ecosystem services in (agro)ecosystems (Barot et al., 2017; Beillouin et al., 2019; Kremen and Miles, 2012; Tilman et al., 2001). In agriculture, crop diversification has been promoted as a way to increase resource use efficiency, improve soils, and mitigate the spread of pests and diseases (Duru et al., 2015b; Malézieux, 2012), and has been found to stabilize food production over time (Renard and Tilman, 2019). Implementing diversification measures, however, requires a different approach to field-level crop management than the typical monocultural system, and therefore requires a rethinking of how the notion of a ‘field’ is defined. Additionally, fitting diversified production systems within current industrial agricultural paradigms presents many challenges and uncertainties.

Conceptually, definitions of ‘diversity’ differ between farming and research contexts, and a unified understanding of the concept is lacking (Hufnagel et al., 2020). How to both qualify and quantify diversity at field and farm levels are open questions. Synthesizing actionable knowledge from research on the relationships between crop diversity and ecosystem service delivery, production, and management practices would greatly benefit from the structure of a common framework (Geertsema et al., 2016). For farmers, such a framework could also be useful for guiding the choice and implementation of management practices based on desired ecosystem services. The first objective of this paper is therefore to explore how farming practices mobilize diversity and to integrate these concepts into a common framework.

Practically, farmers encounter socio-technical lock-ins at all levels of production, from field to market, which inhibit and dissuade them from

diversifying (Magrini et al., 2016; Meynard et al., 2018; Roesch-McNally et al., 2018). In addition to technological and marketing support, knowledge on the ecosystem service benefits of crop diversification has been identified as a key lever for helping European farmers overcome these lock-ins (Mawois et al., 2019; Morel et al., 2020; Pelzer et al., 2019). In particular, conventional and specialized farmers have identified that they need this knowledge before they will consider adopting new crops (Morel et al., 2020). Clear evidence of the benefits of combining diversification measures is therefore needed if farmers are expected to move away from large-scale monoculture systems towards more diversified arable fields with more complex management demands (Duru et al., 2015a). Farmers, however, are not the only food system actors facing lock-ins: research agendas are also limited by the influence of specialization in field and market domains (Magrini et al., 2016; Vanloqueren and Baret, 2009). While it is known, generally, that increasing the resolution of diversity within the arable field affects ecological processes in different ways and at different scales (Duru et al., 2015b), how different diversification measures interact to deliver multiplied, cascading, or diminished benefits is less known (Bommarco et al., 2013; Caron et al., 2014; Losey and Vaughan, 2006). The second objective of this paper, therefore, is to examine examples of multi-dimensional diversification in practice, and to analyse the effects of these practices on the delivery of ecosystem services relevant to European farmers.

In Section 2 we present a conceptual framework for classifying what we call the *three dimensions of diversity* that can be leveraged within the arable farm field; these are *time*, *space*, and *genes*. We begin by briefly reviewing current knowledge on the effects of temporal, spatial, and genetic diversity on ecosystem service delivery in arable cropping systems. We then present a heuristic visualization which combines the dimensions into a three-dimensional space, and position field-level management practices within that space. Synthesizing knowledge of the mechanisms behind the effects of each diversity dimension with an understanding of how the dimensions can be mobilized through practical field management provides a necessary framework for understanding how the unit of management—and thereby the fundamental notion of the arable field—can be redefined to promote diversity.

In Section 3 we introduce the empirical cases, two long-term strip cropping experiments conducted in The Netherlands, and explain our data collection and analysis methods. These experiments tested the effects of two-dimensional (genetic and spatial) diversification on the

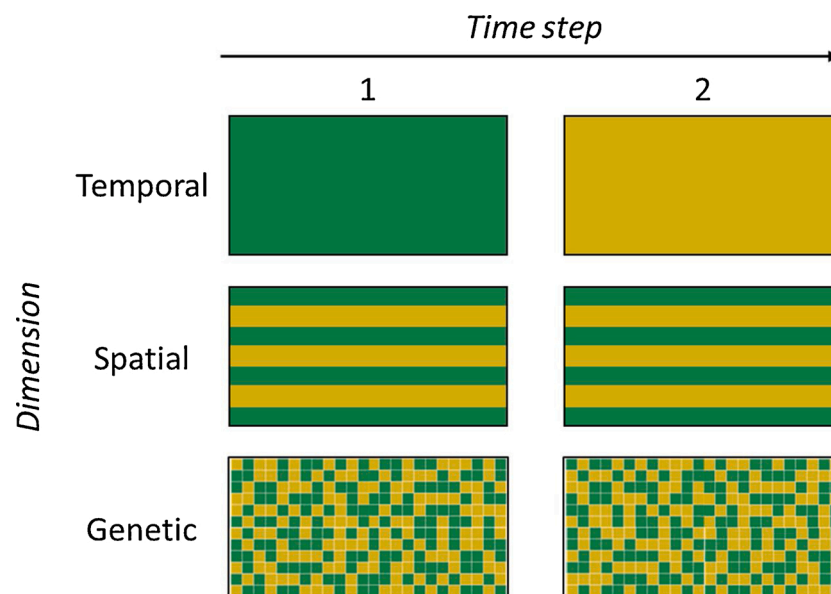


Fig. 1. The three dimensions of diversity that can be mobilized through field management practices, visualized as a field—time unit over two time steps. Each colour represents a different crop or cultivar.

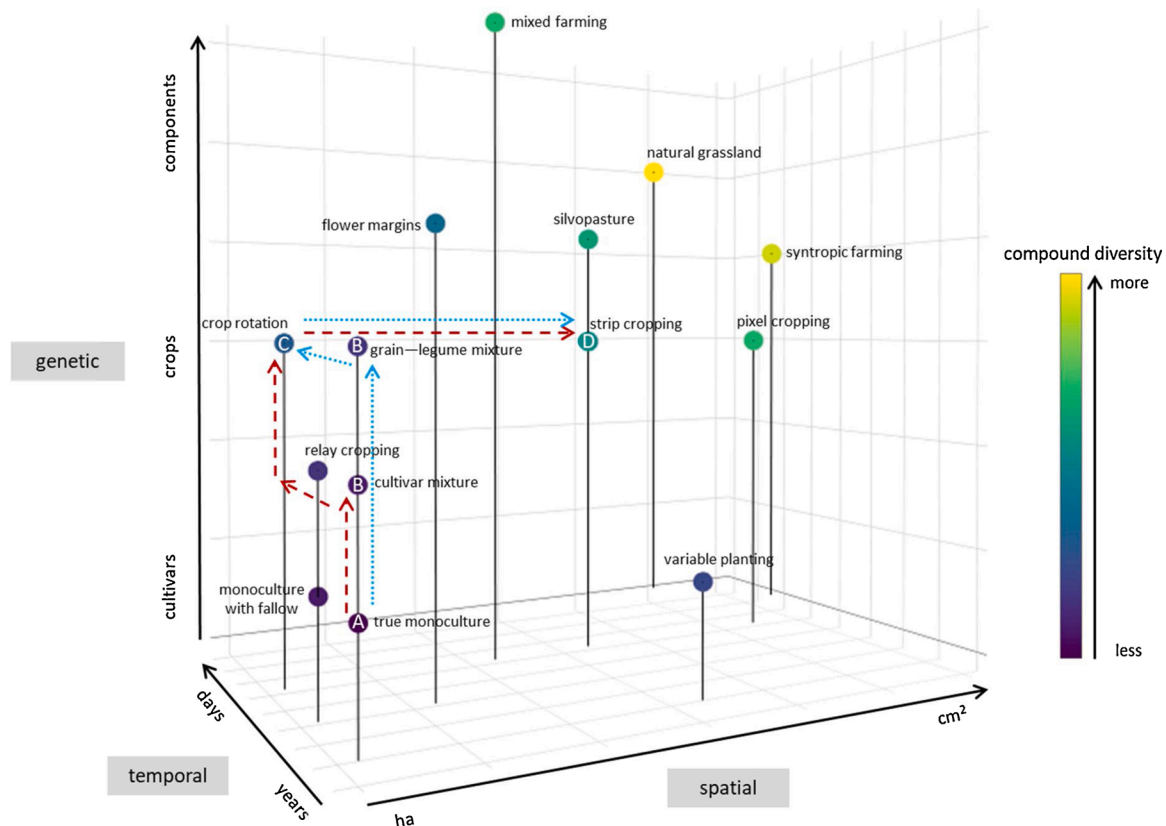


Fig. 2. Heuristic visualization for understanding how field-level farm management practices mobilize the three dimensions of diversity. Diversification measures are positioned within a three-dimensional space where each axis moves from lower to higher heterogeneity (i.e. increasing resolution); scales are qualitative and relative. Starting with a ‘true monoculture’ as an illustrative baseline, the red dashed arrow (potato example) and blue dotted arrow (wheat example) show possible pathways through which a cropping system could be diversified in three dimensions, arriving at the management practice (strip cropping) examined in this paper. Colour scale shows relative compound diversity scores, calculated as the sum of the x, y, and z values for each point.

delivery of two ecosystem services relevant to Dutch farmers: biocontrol potential in wheat (*Triticum aestivum* L.) and late blight mitigation in potato (*Solanum tuberosum* L.). *Phytophthora infestans* (Mont.) de Bary (here forward referred to as *PI*), is an oomycete and the cause of potato late blight, a pernicious disease that infects potato leaves and stems, causing above-ground biomass to die off and tubers to rot. Late blight is of major concern in the Netherlands where conducive conditions are prevalent during the growing season and potatoes are a tremendously important economic industry, and an integrated approach to control is needed (Haverkort et al., 2008; Lammerts van Bueren et al., 2008; Pacilly et al., 2018, 2019). Cereals are also an important crop in the Netherlands, and in cereals aphids are an abundant pest that can cause substantial yield losses—losses that are projected to increase concurrently with climate change (Dedryver et al., 2010; Deutsch et al., 2018; Tatchell, 1989). Like other insect pests, control of aphids is enhanced by the biocontrol provided by natural enemies present in the agroecosystem (Hatt et al., 2017). In both experiment cases, we hypothesized that mobilizing multiple dimensions of diversity simultaneously, i.e. ‘stacking’ diversity measures in the arable field, would result in increasing returns in the form of enhanced ecosystem service delivery (disease mitigation and biocontrol potential) compared to a monoculture.

In Section 4 we present the results of the two empirical cases, and in Section 5 we unpack the results within the frame of the three-dimensional diversity concept, reflecting on the stacking diversity—ecosystem service hypothesis in light of the two-dimensional diversity examples. We conclude the discussion with a theoretical examination of the implications and prospects of mobilizing all three diversity dimensions in concert —i.e. redefining the composition, configuration,

and management of the arable field.

2. Conceptualizing three-dimensional diversity

2.1. Temporal, spatial, and genetic diversity

Taking a ‘true monoculture’ (the same crop cultivar planted in the same field every year) as an illustrative baseline, diversity can be introduced to the arable field in numerous ways, all of which can be categorized in terms of *temporal*, *spatial*, or *genetic* diversification. Following Kremen and Miles (2012) and Wezel et al. (2014), we refer to these categories as the *three dimensions* of diversification in agroecosystems. Increasing diversity in each dimension involves practices that increase the number of crop cultivars, species, or farm components (e.g. trees, livestock) in a field within a given unit of time (i.e. a field—time unit), and implies an increase in the resolution at which those practices are implemented (Fig. 1). Higher resolution is here equated with greater heterogeneity within the field—time unit, qualified by a reduction in the size of the smallest homogenous unit within that field. Homogenous units within the field (areas planted with a single crop species and cultivar) could range in size and shape from several hectares, to strips of several crop rows, or to small ‘pixels’ containing an individual plant or a cluster of plants. Increasing the resolution of diversity in each dimension is known to have different effects on ecosystem service delivery in agricultural contexts, which can be explained by differences (and sometimes overlaps) in the fundamental ecological mechanisms relevant to and activated at temporal, spatial, and genetic scales.

Crop rotation—sowing fields with a different crop each year in a pre-

determined sequence of two or more years—is a commonly employed method of diversification. The resulting *temporal* diversity is known to benefit agroecosystems by breaking transmission cycles of soil- and residue-borne pathogens, and overwintering pests; this is paramount to the underlying rationale for using rotations (Leoni et al., 2015). Additionally, crops access, exploit, and influence soil resources differently. By rotating crops with differing nutrient demands, rooting behaviours, residue legacies, and mechanical cultivation needs, soil damage can be mitigated and soil resources maintained (Dogliotti et al., 2003; Venter et al., 2016), and weed suppression improved (Weisberger et al., 2019).

Genetic diversity is commonly studied and implemented in agricultural settings as cultivar or species mixtures (e.g. cereal—legume) uniformly sown and managed like a sole crop. Resource capture and use efficiencies are regularly found to be higher in mixtures than in sole crops, due to niche complementarity and facilitation (Hauggaard-Nielsen et al., 2008; Pelzer et al., 2012). Mixtures of species and cultivars are also known to have lower pest and disease infestations relative to monocultures, in part because mixing host and non-host species or cultivars dilutes the concentration of resources and disrupts the movement of pests and diseases through a crop stand (Lopes et al., 2015; Skelsey et al., 2005; Zhu et al., 2000). The diversity of habitats and resources provided by species mixtures may also support a greater abundance and diversity of natural enemies which contribute to the biocontrol of pests (Isbell et al., 2017; Poveda et al., 2008).

Although less well studied and less commonly applied in industrial arable fields, *spatial* diversification measures are known to provide similar ecosystem services as genetic measures within agroecosystems. Recent meta-analyses show that row and strip intercropping can substantially increase crop yields through niche differentiation (van Oort et al., 2020; Yu et al., 2015), as well as reduce disease incidence (Zhang et al., 2019) and pest infestation (Tajmiri et al., 2017). Similar to the mechanisms at work in genetic mixtures, spatial heterogeneity works to regulate pest and disease spread by mobilizing barrier effects which disrupt movement and dilute resources, as well as by creating micro climate effects (Hatt et al., 2018).

2.2. Visualizing a three-dimensional diversification space

Visualizing the diversification space helps to disentangle the dimensions of diversity at play in arable systems as they are activated through the implementation of farming practices, and several authors have offered useful approaches for doing this (e.g. Brooker et al., 2015; Duru et al., 2015b; Kremen et al., 2012; Wezel et al., 2014). Drawing on these examples, we propose a new heuristic visualization which illustrates the way field-level practices mobilize the three diversity dimensions. We visualize diversification as a three-dimensional space, and position farming practices within it (Fig. 2). Here we consider ‘true monoculture’ (the same crop planted in the same field every year) as an illustrative baseline, positioned at the spatial (x), temporal (y), genetic (z) point [1, 1, 1]. Moving up the axis of each dimension implies increasing field-level heterogeneity through practices that increase the resolution of diversification; the farther from the baseline of the figure, the more diverse the field—time unit and the higher the resolution of diversification. The total diversity of each practice has here been calculated simply as the sum of the three axis values to give a compound diversity score. Scores on all axes should be considered qualitative and relative.

In Fig. 2 we have traced two pathways illustrative of management practices which might be chosen by a farmer seeking to diversify arable fields, and which are later discussed in the empirical cases. In the example outlined by the red dashed arrow (Fig. 2, points A–D), we start with a hypothetical (albeit unrealistic) scenario in which the true monoculture (Fig. 2, point A) represents a field where a single cultivar of potato is grown season after season, year after year. Diversification can occur in three ways. First, introducing an additional cultivar, species, or component to the field enables a farmer to increase genetic diversity. In

the hypothetical continuous potato system, adding the second potato cultivar and sowing as a homogenous mixture results in a move up the genetic axis while maintaining the baseline position on the spatial and temporal axes (Fig. 2, red dashed arrow to point B).

Next, the baseline can be extended on the temporal axis by introducing a fallow, new species, or additional components over time. The addition of a fallow in the all-potato rotation would move the point up only on the temporal axis. By introducing a crop rotation of two or more crop species rotated sequentially over cropping seasons or years, the point moves up both the temporal and genetic axes (Fig. 2, red arrows to point C).

Finally, to diversify the system spatially, a farmer can introduce methods that increase the resolution at which multiple crop cultivars, species, or farm components are physically arranged within the field at a given point in time. In the potato example, point C can be moved up the spatial axis by implementing a practice that delineates spatially explicit multi-crop arrangements within the field (Fig. 2, red arrow to point D). Here the illustrative practice is strip cropping, in which it is assumed that crops are grown in multi-row strips in an alternating pattern of at least two crops.

We posit that visualizing the diversification space can help to disentangle how field-level practices function to deliver agroecosystem services: by recognizing which dimension(s) of diversity are activated when a farming practice is implemented, results may be analysed and understood through the lens of the mechanisms active in each dimension. We propose that this heuristic, together with knowledge of the mechanisms behind the ecosystem service delivery outcomes of each diversification dimension, be used to unpack experimental results and to position such results within the conceptual premise of redefining the arable field. We will demonstrate how this may be done with empirical examples in Sections 4 and 5.

3. Empirical cases: materials and methods

To test the stacking diversity hypothesis and illustrate an application of the conceptual framework presented in Section 2, we analysed the effects of multi-dimensional crop diversification on two ecosystem service indicators in arable cropping systems using multi-year data (2010–2017) from two long-term organic systems experiments in the Netherlands. The two empirical cases analysed are illustrated in Fig. 2 as the red dashed arrow (potato case) and the blue dotted arrow (wheat case). In both cases, two dimensions of diversity were mobilized through the management practices of strip cropping (spatial diversity) and crop mixtures (genetic diversity). Both systems experiments followed diverse crop rotations, however we do not examine the temporal dimension in this analysis.

3.1. Experiment sites

The experiments were located at two Wageningen University & Research experimental stations: the Field Lab for Agroecology and Technology in Lelystad (52°32′30″N, 5°34′20″E) and the Droevendaal Experimental Farm in Wageningen (51°59′30″N, 5°39′50″E). Both experiments were managed according to Dutch organic standards and regulations (Skal, 2020). For both potato and wheat, three experimental treatments were tested: 1) large-scale sole-cropped reference fields (REF), 2) sole-crop, single cultivar strips (STRIP), and 3) mixed-species or mixed-cultivar strips (STRIP_MIX). For potato, the STRIP treatment was planted with the non-PI resistant cultivar Agria, and mixed strips consisted of a cultivar mixture which included one non-PI resistant cultivar (Agria) and two PI-semi-resistant cultivars (Carolus and Alouette). For wheat, mixed strips were sown as a polyculture composed of a cross-composite population of spring wheat and faba bean (*Vicia faba* L.). In Lelystad, only REF and STRIP potato treatments were present, and in Wageningen all three treatments were tested in both potato and wheat. In 2017 in Wageningen, the additional experimental factor of

Table 1

Environmental characteristics and experiment details, including mean yields per treatment each year, at the two experiment sites (the Field Lab for Agroecology and Technology in Lelystad and Droevendaal Experimental Farm in Wageningen, both in the Netherlands), 2010–2017.

Site characteristics	Lelystad (2010–2016)	Wageningen (2015–2017)		
Soil texture	Light clay / sandy clay loam	Loamy sand		
OM content (%)	4.29	3		
Annual temp in °C (average during study timespan)	10	11		
Annual rainfall in mm (average during study timespan)	846	973		
Crop rotation	potato, grass—clover, cabbage, spring wheat, carrot, faba bean—spring wheat mixture	potato, grass—clover, grass—clover, winter oil seed rape, winter triticale, spring wheat		
Strip dimensions (length x width)	80–125 m x 3.15 m	240m x 3m		
Reference field dimensions	2–3 ha	0.5–3 ha		
Tillage practice	Non-inversion	Minimal tillage		
Crop Yields	potato yield (t ha ⁻¹)		wheat yield (t ha ⁻¹)	
		Lelystad 2010–2016	Wageningen 2015–2017	
	Large-scale reference	29.09 [†]	37.14	2–3 [*]
	STRIP_3 m	30.39	41.23	2.68
	STRIP_MIX_3 m	32.72	47.65	1.71
	STRIP_6 m	NA	37.41	NA
	STRIP_MIX_6 m	NA	43.55	NA

* Reference plot yields were not measured, farmer estimated 2–3 t^{ha}⁻¹ average.

[†] Reference yields only recorded in 2014 and 2016.

Table 2

Infection scoring method (unit of measurement) and number of late blight (*P. infestans*) observations made in potato crops at the Lelystad and Wageningen field experiments in the Netherlands, 2010–2017.

Year	Infection unit measured	Number of experiment blocks	Number of observation rounds	Plants inspected first round*	Support (total plant inspections)
Lelystad					
2010	leaf area affected (%)	1	1	30	180
2011	leaf area affected (%)	3	1	25	450
2012	leaf area affected (%)	2	2	35	1015
2013	plants affected (%)	2	6 [†]	100	700
2014	severity (%)	2	3	35	5180
2015	severity (%)	2	3	35	2240
2016	severity (%)	2	6 [‡]	35	2730
Wageningen					
2017	infected leaflets per m ²	3	12	360	3084

*Total number of plants inspected per round decreased throughout the season as plots were terminated, having reached the regulatory threshold for late blight infection. As long as all plots were not yet terminated, the same number of plants was inspected in subsequent rounds as in the first round.

[†]During the first five observation rounds, no *PI* infections were encountered.

[‡]REF field was terminated after first assessment.

strip width was introduced in the potato plots, and two strip widths were tested (3 m and 6 m) in comparison to the large-scale reference. Basic experimental details and environmental characteristics at each study site, including mean yields obtained per treatment, are outlined in Table 1. Maps of the experimental layouts are provided in the Appendix A, Fig. A1.

3.2. Data collection

3.2.1. *PI* infestation in potato

Over the multiple years of the experiments, different scoring methods, all using visual observation, were employed to assess *PI* infection: leaf area affected (%), plants affected (%), severity (%), and infected leaflets per m² (for explanations of these metrics, see: EPPO, 2008; Madden et al., 2007). Within years, the same scoring method was used in both the strips and the REF. Only plants of the non-*PI* resistant cultivar were scored for disease infection. At Wageningen in 2017, the same plants observed in the first round were then revisited at each subsequent round until the plot was terminated. Following Dutch regulations for the management of *PI* (De Minister van Landbouw, Natuurbeheer en Visserij, 2017), plants were terminated when plot-level infection severity reached 20 infected leaflets per m². The methods used and number of *PI* observations made each year and at each experimental location are outlined in Table 2.

3.2.2. Epigeic natural enemies of aphids in wheat

As an indicator of biocontrol potential for aphids in wheat, we assessed the prevalence and diversity of their epigeic natural enemies (NE). NE were captured and identified at the Wageningen experiment across three growing seasons (2015–2017) in the two strip treatments (STRIP and STRIP_MIX), and in the REF, using pitfall trapping. Pitfall traps were constructed using a transparent plastic cup (8.5 cm diameter) placed in the soil so that the rim of the cup was level with the soil surface. Cups were filled with approximately 100 ml of water mixed with one drop of neutral soap, covered with a plastic roof (12.5 cm diameter) positioned 2 cm above the soil surface, and left in the field for 2–5 days, depending on the weather conditions (at cooler temperatures, traps were left out longer) (Fig. 3). In the strip-cropped treatments, one pitfall trap was placed in each experimental plot ($n = 6$ per treatment). In the large-scale monoculture field, pitfalls were placed within a strata 34 m from the field edge (the centre of the field), with six replicates in 2015 and 2016 and four replicates in 2017.

Arthropods captured in the pitfall traps were preserved in 70 % ethanol and identified in the laboratory. Only known predators to aphids (following Schmidt et al., 2003) were identified and counted. These were: adult and larval ladybeetles (*Coccinellidae*), hoverfly larvae (*Syrphidae*), adult and larval lacewings (*Chrysopidae*), parasitoid wasps (*Hymenoptera*), spiders (*Araneae*), harvestmen (*Opiliones*), adult and

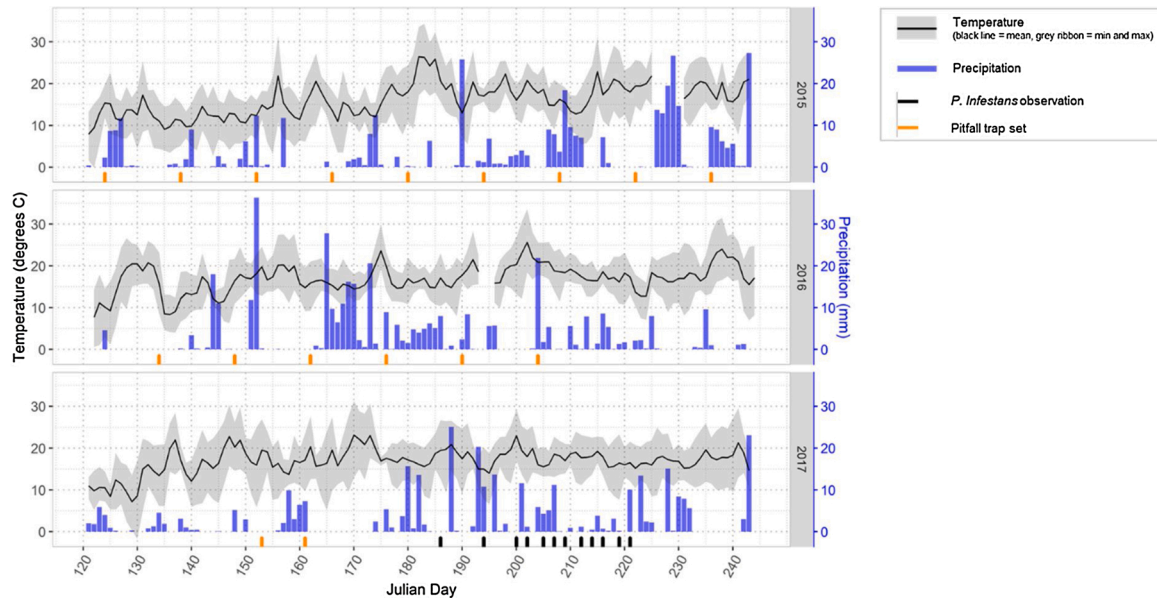


Fig. 3. Weather at the Wageningen site during experiment observations, 2015–2017. Orange ticks on the x axes mark pitfall trapping dates, black ticks mark *PI* observation dates. Black line shows mean temperature (degrees Celsius), grey ribbons span daily minimum and maximum temperatures (degrees Celsius), and blue bars are the sum daily precipitation (mm). Data obtained from the Royal Netherlands Meteorological Institute (KNMI) and the weather station De Veenkampen operated by Wageningen University.

larval carabids (*Carabidae*), and adult and larval rove beetles (*Staphylinidae*). Parasitoid wasps, spiders, and harvestmen were identified to the level of Order; ladybeetles, hoverflies, lacewings, and rove beetles to Family; and carabids to Genus.

Three indicators were used to assess the prevalence and diversity of NE in the pitfall catches: activity density (as an indicator of abundance), species richness, and evenness (Dainese et al., 2019). Activity density was calculated as catch per day by dividing the total number of arthropods in the pitfall trap by the number of days the trap was in the field. Species richness was calculated as the number of unique taxa (at the levels described in the above paragraph) identified in each sample. The evenness of the distribution of taxa in each sample was assessed using the Shannon diversity index, calculated with the *vegan* package (Oksanen et al., 2019) in R (version 3.5.0, team, 2018).

3.3. Data analysis

3.3.1. Multi-year comparisons between treatments: *PI* incidence and NE indices

To compare the effect of the spatial and genetic experimental factors on both disease incidence and NE indices across the multiple years of the strip cropping experiments, we used a clustered Wilcoxon rank sum test. This is a conservative non-parametric test suited for comparing two populations of clustered but independent data, which we performed

with the *clusrank* package (Jiang, 2018) in R. Data were clustered by observation date and experiment block, meaning that we only compared observations for which there were data collected in both the REF and STRIP treatments, and for NE in wheat also in the STRIP_MIX treatment, on the same date and in the same experiment block.

In all clustered Wilcoxon rank sum tests performed, mean ranks of the target indicator, calculated at the experiment block level, were compared between treatments for each cluster. The test can only compare two groups, so we first assessed differences between the REF and STRIP treatments to discern effects of spatial diversity on the target indicator. For disease incidence in potato, this was the only test we conducted, as only REF and STRIP treatments were present at the Lelystad experiment where we had multiple years of *PI* data (2010–2016). With the pitfall catch data, we then conducted a second test comparing the STRIP and STRIP_MIX treatments to assess the potential effect of genetic diversity measures. A significant *p*-value (<0.05) resulting from the test supports the hypothesis that at any given observation moment, the target indicator value in treatment *a* (REF or STRIP) would be significantly different than in treatment *b* (STRIP or STRIP_MIX) for observations conducted in the same experiment block.

3.3.2. Within-year assessment of rate of *PI* spread, 2017

We analysed the rate of late blight disease spread in STRIP and STRIP_MIX treatments compared to the REF within a single season and

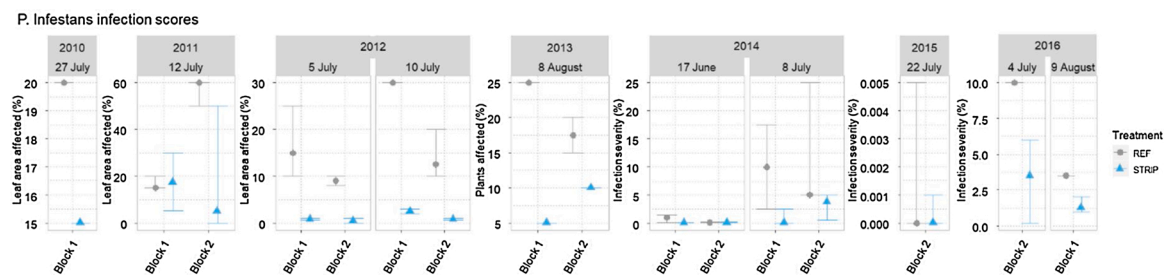


Fig. 4. *PI* infection scores in large-scale potato reference fields (REF, grey circles) compared to scores in strips (STRIP, blue triangles) for each observation date across all experiment years (2010–2016) at the Lelystad experiment. Data are paired by cluster (observation date and experiment block). Points show median scores and bars mark minimum and maximum recorded scores for each cluster.

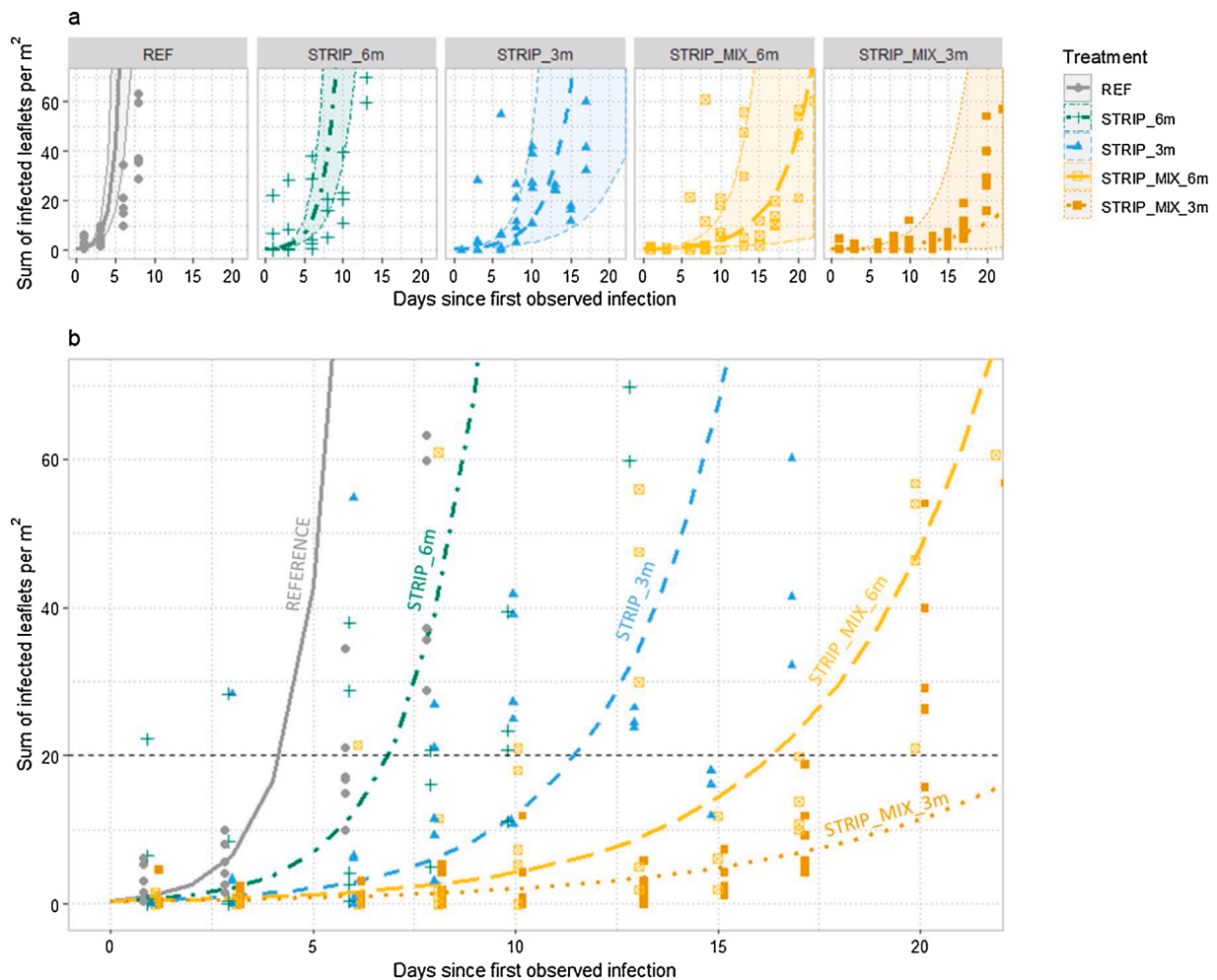


Fig. 5. *PI* infection in potato over time during the 2017 growing season at the Wageningen experiment in the five treatments: large-scale reference monoculture (REF, grey circles), single cultivar 6 m strips (STRIP_6 m, green plus signs), single cultivar 3 m strips (STRIP_3 m, blue triangles), mixed cultivar 6 m strips (STRIP_MIX_6 m, yellow boxes), and mixed cultivar 3 m strips (STRIP_MIX_3 m orange squares). Large bold lines (a and b) show predicted infection per treatment calculated on mean rates modelled with a linear mixed effects model. Shaded transparent ribbons outlined by thinner lines (a) show the standard error of the predicted infection per treatment based on the model. The horizontal black dashed line (b) marks the infection threshold (20 infected leaflets per m²) at which potato fields must be burned, according to Dutch regulation.

location, 2017 at Wageningen. In this year the experiment set-up included the additional factor of strip width, with two levels (3 m and 6 m). For this analysis we first log-transformed (using the natural logarithm) the disease incidence data, and then calculated the rate of disease spread at the plot level as the difference in disease score between the observation date and the date of the first observed infection. We then used a linear mixed-effects model to test the effect of the treatment factors on those rates (Zuur et al., 2009). In the model we included both spatial (strip width) and genetic (single or mixed cultivar) factors as fixed factors. Experimental plot was nested within field as a random effect in the model to account for potential variability in field conditions. We conducted multiple comparison of means post-hoc tests on the model to make pairwise comparisons between effects of treatment factors on rates of disease spread, with a significant effect determined for p -values <0.05. Modelling analyses were conducted using the *lme4* package (Bates et al., 2015) in R, and post-hoc tests were conducted using the *multcomp* package (Hothorn et al., 2008), also in R.

4. Results

4.1. *PI* infestation in potato

In the multi-year (2010–2016) comparison of *PI* infection scores in

the STRIP vs. REF potato treatments at the Lelystad experiment, we found that median *PI* infestation scores were lower for STRIP than for REF in 15 out of 16 paired observation clusters (Fig. 4). The clustered Wilcoxon rank sum test of the infection scores in STRIP vs. REF across all years showed the difference to be significant ($p < 0.001$).

The comparison of plot-level *PI* infection between potato treatments during the 2017 growing season at Wageningen showed a significant effect of both spatial arrangement and cultivar mixing on the rate of disease spread. When the two treatment factors were differentiated as separate fixed factors in the linear mixed model, the post-hoc pairwise comparisons showed that rate of disease spread was significantly lower in the mixed-cultivar treatments (genetic factor) compared to the monocultural REF ($p = 0.0238$), and that only the narrower strip width (3 m, spatial factor) showed significantly lower disease spread compared to the REF treatment ($p = 0.0087$). The lowest rates of disease spread were observed when the two treatment factors were combined (Fig. 5).

4.2. Epigeic natural enemies of aphids in wheat

When analysed at the level of individual NE groups, we found that across the three years of pitfall trapping in wheat at the Wageningen experiment, there was significantly higher NE activity density (catch per day) in the two strip treatments compared to the REF for all NE groups

Table 3

Effect of spatial and genetic crop diversity on activity density (an indicator of abundance), richness, and evenness of epigeic natural enemies of aphids in wheat collected by pitfall trapping at the Wageningen experiment from 2015–2017. Treatments were compared using a clustered Wilcoxon rank sum test, and data were clustered by observation date and experiment block. Only data for which there were paired observations in both treatments at each sampling date were included in the analysis.

	Strip vs. Ref		Strip vs. Strip_Mix	
	p value	effect direction	p value	effect direction
Total activity density	0.298	NA	0.846	NA
spiders	< 0.001	STRIP > REF	0.629	NA
rove beetles	< 0.001	STRIP > REF	0.547	NA
harvestmen	< 0.001	STRIP > REF	0.177	NA
carabids (non- <i>Pterostichus</i>)	< 0.001	STRIP > REF	0.157	NA
carabids (<i>Pterostichus</i>)	< 0.001	REF > STRIP	0.230	NA
other NE	< 0.001	STRIP > REF	0.978	NA
Richness	< 0.001	STRIP > REF	0.402	NA
Evenness (Shannon diversity)	< 0.001	STRIP > REF	0.586	NA

except *Pterostichus* carabids (Table 3, Appendix A Fig. A5). For *Pterostichus*, catches were significantly larger in the REF. The clustered Wilcoxon rank sum test also showed there to be no significant difference in catches between STRIP and STRIP_MIX treatments for any of the NE groups (Table 3).

When all NE groups were aggregated, there was no significant difference in activity density between strip treatments and the reference (Table 3). Catches in REF on dates when *Pterostichus* carabids were abundant consistently tipped total NE counts above those of the STRIP and STRIP_MIX catches. STRIP and STRIP_MIX had consistently higher diversity index scores across all experiment years (Table 3). Compared to the large-scale reference, strips had both a greater number of unique taxa, and more evenness in the distribution of species as indicated by higher Shannon diversity index scores (Fig. 6). Added within-strip genetic diversity did not improve NE diversity scores in the STRIP_MIX compared to the STRIP (Table 3).

5. Discussion

5.1. Stacking diversity: empirical evidence

We hypothesized that stacking multiple diversity dimensions would return increasing benefits in the form of enhanced ecosystem service

delivery in arable contexts. With two examples of strip and mixed intercropping in the Netherlands, we investigated the effects of activating multiple dimensions of diversity on the delivery of two ecosystem services relevant to Dutch farmers, namely disease mitigation in potato and biocontrol potential in wheat. We found the effect of increasing spatial heterogeneity to be beneficial. Only in the potato case, the combined effect of spatial and genetic diversity measures resulted in the greatest benefit in the form of reduced late blight incidence and slowed disease spread. In the case of biocontrol in wheat, the addition of genetic diversity did not appear to have added value over spatial heterogeneity alone for the measured indicators. We frame our discussion of these empirical findings within the multi-dimensional diversity framework presented in Section 2.

5.1.1. Disease control in potato

The positive effect of spatial diversity on disease mitigation in potato was clearly illustrated in the seven years of experiment data from Lelystad. *PI* infection scores in the STRIP treatment were consistently lower than in the associated large-scale REF fields across all years, a result in accordance with previous studies on spatial diversity and *PI* (Bouws and Finckh, 2008; Skelsey et al., 2009, 2010). These studies concluded that a combination of physical barrier effects and host dilution were the most likely causes of lower disease incidence in

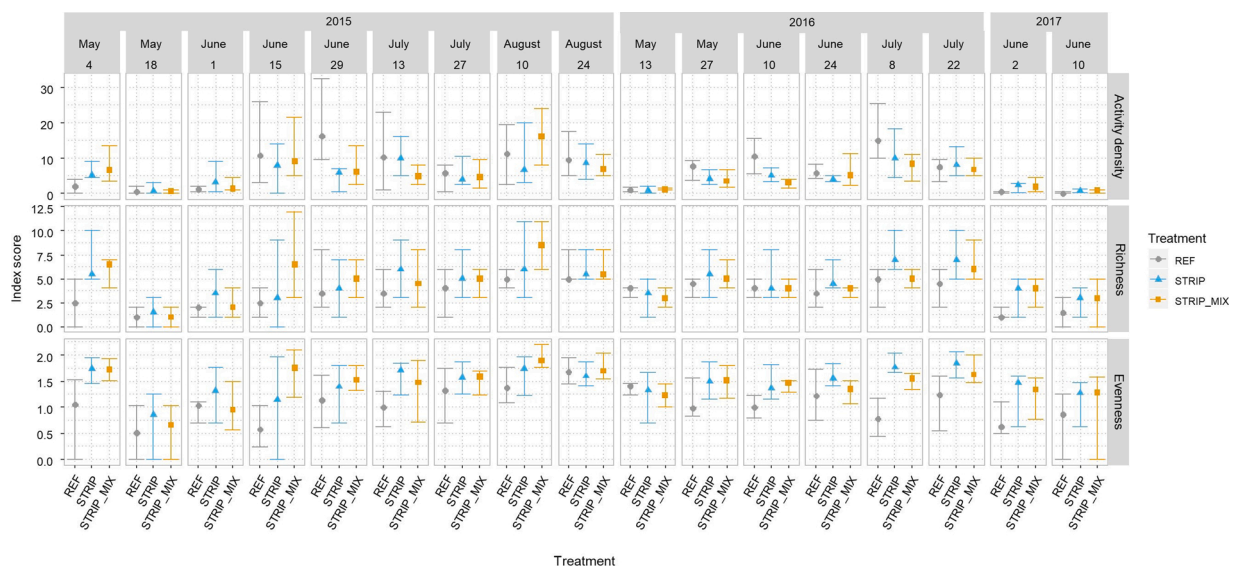


Fig. 6. Activity density (catch per day, top), species richness (number of unique taxa, middle), and species evenness (Shannon diversity, bottom) of epigeic natural enemies of aphids in wheat collected by pitfall trapping in the three treatments (REF, grey circles; STRIP, blue triangles; STRIP_MIX, orange squares) at the Wageningen experiment for each paired observation date from 2015–2017. Data are presented as clustered by date (medians aggregated across experiment blocks per date) to simplify the figure; in the statistical analysis data were clustered by observation date and experiment block. Points show median scores and bars show the range (minimum and maximum) in catches per cluster.

strip-cropped potatoes compared to large-scale monocultures. The physical barrier effect is not a likely explanation for the observed disease mitigation at the Lelystad experiment, since the strips there were planted parallel to the predominant wind direction (contrary to Bouws and Finckh, 2008). Our results imply therefore that by increasing spatial diversity, disease mitigation was obtained through host dilution.

When genetic diversity was added within the potato strip arrangement in the form of cultivar mixtures, we found the additional benefit that the rate of *PI* spread in susceptible plants at the plot level was lowered. The relative rate of disease spread was least in the STRIP_MIX treatments compared to both STRIP and REF plots at Wageningen in 2017, confirming our hypothesis that increased heterogeneity, expressed as the stacking of multiple diversity dimensions, would increase the delivery of the target ecosystem service. The effect of genetic mixing can be explained by the mechanisms at play in spatial diversity, but at plant level rather than crop stand level. Host dilution and barrier effects are both enhanced by the fine resolution mixing of cultivars at the plant level, leading to a greater loss of compatible inoculum in mixtures with contrasting *PI* resistance genes than in pure stands (Andriveau et al., 2003; Skelsey et al., 2009, 2005). At Wageningen, it appears that mixing within the strip reduced the likelihood of disease spread at the plant level, while adjacent non-host strips impeded the dispersal of any remaining spores that did propagate, leading to an overall greater reduction in disease severity at the plot level.

5.1.2. Biocontrol potential in wheat

Diversification measures that enhance biocontrol potential act from both the bottom up and the top down: by making the cropping system less attractive or less hospitable to pests, and by accommodating predators. The data collected in the strip cropping experiment at Wageningen only allowed us to analyse top-down effects since aphids were not monitored. Our findings reflect several recent comprehensive studies which all show that crop diversity at higher resolutions—whether at the plot, field, or landscape scale—has a positive impact on biodiversity in general and on pest suppression potential specifically (Dainese et al., 2019; Fahrig et al., 2015; Iverson et al., 2014; Lichtenberg et al., 2017; Sirami et al., 2019). However, our results showed the implemented spatial and genetic diversification measures to have differing impacts on top-down pest control mechanisms, and the findings did not support our stacking diversity hypothesis.

In our experiment, the effect of spatial diversity on NE activity density was evident in the significantly larger catches observed in the STRIP treatments compared to the REF for all but one NE group. This result is in line with previous studies which conclude that spatial diversity supports NE populations by providing an array of host, feed, shelter, and habitat sources throughout the cropping season (Ratnadass et al., 2012), as well as refuge during disturbances such as crop cultivation activities (Dassou and Tixier, 2016). Only the *Pterostichus* carabid beetle was found to be more abundant in the REF system. Although contradictory to Thomas et al. (2006) who found *Pterostichus* to prefer less dense crop stands, our finding is in line with Allema et al. (2019) who showed that *Pterostichus* preferentially occupy large-scale cereal monocultures. While maintaining an abundance of NE is important for top-down aphid control, it has recently been shown that diversity indicators such as species richness and evenness may be more influential predictors of biocontrol potential than abundance (Dainese et al., 2019). Promisingly, our experiment results showed spatial crop diversity had a strong positive impact on both the richness and evenness of the epigeic NE community, a finding that could be explained in part by the work of Allema et al. (2015) who found that different arthropods had preferences for different vegetation types. Diversity of NE presumably also implies a higher likelihood that a mix of specialized and generalist predators are present in the cropping system, which is important for aphid control (Snyder and Ives, 2003).

We expected that the addition of increased genetic diversity within the strip arrangement would further improve NE abundance and

diversity. However, our experiment results showed no significant difference in NE activity density nor diversity indices between the STRIP and STRIP_MIX systems, indicating that stacking genetic diversity did not add value over what was already achieved via spatial diversification alone. This result is corroborated in a review which found no cases in which mixed intercropping of wheat increased the presence of pest predators (Lopes et al., 2016), however contradicts the ‘enemy hypothesis’ (Root, 1973) and a meta-analysis assessing other crops (Dassou and Tixier, 2016). The fact that we did not see added value of genetic mixing within the strip arrangement could imply that at the field scale, the spatial diversity of the strip arrangement had a stronger influence on epigeic arthropod movement patterns than the plant-level genetic heterogeneity of the within-strip crop mixing, as has been found at the landscape scale (Martin et al., 2019).

5.2. 3-D Diversity: implications and prospects

5.2.1. Managing complexity

Redefining the agricultural field—that is, changing the way compositions of crops and cultivars are arranged on a farm in space and time—will result in agricultural fields that look different, are more complex, and require new management strategies, technologies, and institutional frameworks. Moving from control-based management towards ecological management positions farmers in a role that is less about managing inputs and outputs and more about facilitating and collaborating with agroecological processes to achieve harvestable yields (Robertson et al., 2014; Storkey et al., 2015; Tittonell et al., 2016). Such a shift could mean that farmers are relieved of selected management burdens as agroecosystems are increasingly able to self-regulate (Van Apeldoorn et al., 2011). However, it could also position farmers in a management role that becomes vastly more complex and knowledge-intensive, and potentially expensive (Rosa-Schleich et al., 2019). Before farmers can be expected to engage in such a transition, benefits and drawbacks of a move towards more complexity must be further investigated.

Promisingly, the results of the empirical cases presented here indicate that moderate changes to field design and management can return substantial benefits to farmers in the form of enhanced ecosystem service delivery. In both the potato and wheat examples, introducing spatial diversity alone through strip cropping was sufficient to increase disease suppression and biocontrol potential, respectively. The robustness of the spatial effect implies that farmers can be flexible in how they implement strip cropping, and do not necessarily need special equipment to do so.

At Lelystad, disease mitigation was enhanced despite the arrangement of strips parallel to the dominant wind direction. Additionally, at the Wageningen experiment in 2017, we found that both 3 m and 6 m strip widths showed lower rates of disease spread than the REF. These results indicate that for disease control, strip width can be adapted to fit mechanical capabilities, and strips can be arranged in the field without the constraint of having to be aligned in a particular direction for the benefits to be realized. Further studies on disease spread in relation to strip width and wind direction would be useful for confirming this flexibility.

Although it implies a more complex management approach, namely in terms of post-harvest processing and marketing, the added disease mitigation benefit of introducing genetic diversity within potato strips should not be discounted. Sanitary regulations in the Netherlands require defoliating a potato crop when the severity of a *PI* infestation reaches 7–10 % (De Minister van Landbouw, Natuurbeheer en Visserij, 2017). Under organic conditions this is done by mechanical or thermal haulm destruction. A potato stand may produce 700–900 kg of potato fresh weight per hectare per day during the tuber filling stage (Möller et al., 2006), and at defoliation, tuber filling is halted. Delaying the time of defoliation therefore has a strong effect on the quantity and quality (in terms of tuber size) of a potato harvest. Following regulation, the farmer

at Wageningen in 2017 defoliated the STRIP_MIX treatment plots two to five days later than the STRIP treatment plots, and higher yields were indeed recorded in the STRIP_MIX plots compared to the STRIP plots (Table 1). From a farmer's perspective, it follows that both delaying the onset of the disease and slowing down its spread—together delaying the termination of the crop—are important objectives in the management of *PI*, and strip cropping offers a robust approach to achieving this.

Given the potential yield benefits of having a potato stand with less late blight infection, one might ask why a farmer would not forgo the mixing of *PI*-resistant with susceptible cultivars and instead plant strips of only the resistant cultivar. This would be simpler, by not necessitating post-harvest sorting of cultivars. However, late blight resistance is only one of the criteria for which potatoes are bred (Bueren et al., 2018), and only one trait that farmers weigh when choosing which cultivars to plant. Production potential and consumer preference are also high priorities, both of which tend to be better for the more established non-resistant potato cultivars like Agria. In The Netherlands, the consumer preferences driving potato markets are relatively narrow and traditional, and it can be hard for farmers to sell newer, less well-known varieties like the Carolus or Alouette. Common practice for organic farmers in The Netherlands is therefore to plant some of each cultivar in order to reduce the risk of *PI* while also ensuring marketability of the harvest (Pacilly et al., 2019). The experiment in Wageningen reflected these management considerations by taking the susceptible Agria cultivar as the reference.

For biocontrol enhancement, strip-level diversity was found to give as good results as strips combined with plant-level mixing, making the procurement of specialized mixed-cropping machinery appear unnecessary. However, more effective non-chemical aphid control would require the incorporation of design elements that complementarily undermine aphid reproduction and dispersal, in addition to supporting NE populations. Further studies on pest populations in strip arrangements would be useful for helping farmers optimize strip design for biocontrol.

5.2.2. Theoretical considerations

In our discussion of experimental results, we found the conceptual framework for three-dimensional in-field diversity particularly useful for linking management practice outcomes to diversity-mediated mechanisms by discerning which dimensions (spatial or genetic) were activated. The framework does not, however, illustrate nor quantify response relationships between the three diversity dimensions and ecosystem service delivery. Knowing what happens to ecosystem service delivery when multiple dimensions are mobilized in the field at once is necessary for understanding how to manage farm fields for optimizing the delivery of targeted ecosystem services (Bommarco et al., 2013), how to best make use of inherent in-field diversity (Isbell et al., 2017), and thus how much management complexity is required. Once response relationships between field practices and ecosystem service delivery in each dimension are better understood, the diversification space heuristic may be developed to function as a practical solution space from which farmers could select practices to optimize their combined agronomic and ecological goals (Groot et al., 2010; Groot and Rossing, 2011).

In our own study, we only examined two dimensions: space and genes. Our brief review of diversity effects, however, implies that adding the third dimension—time—to the strip cropping system could add further value to ecosystem service delivery by breaking pest and disease propagation cycles. Yet our findings on stacking spatial and genetic diversity in wheat may indicate that three-dimensional diversity is not necessary to achieve improved provision of certain ecosystem services. Classic examples in ecology, such as the diversity—productivity response in (natural) grasslands (Hector et al., 1999; Tilman et al., 2001), show that increasing diversity only increases productivity up to a saturation point. Asymptotic yield responses to biodiversity increase have been shown in arable agricultural contexts as well (Barot et al., 2017). There is less consensus on the shape of response curves for other ecosystem services, but in the cases of pest and disease suppression in

particular, it is well-known that the magnitude of the diversity effect depends on many additional factors (Bianchi et al., 2006; Isbell et al., 2017; Iverson et al., 2014; Letourneau et al., 2011; Pacilly et al., 2018).

Experimenting with diversification measures at relevant spatial and temporal scales presents challenges to understanding the response relationships between diversity dimensions and ecosystem service delivery. With dispersal distances of 100 m for aphid NE to tens of kilometres for *PI* (Skelsey et al., 2010; Steingröver et al., 2010), variables such as those analysed here require large-scale reference fields. Due to resource constraints, the large-scale monoculture reference plots used in the presented studies were not replicated and not necessarily in the same field as the strip treatments. Additionally, diversity appears to beget diversity (Reckling et al., 2018); in our spatially and genetically diverse treatments we tended to see more variability in the data than in the large-scale monocultural references. While statistical methods such as those employed in our analysis are able to accommodate incomplete block designs, diversity, and random variation, the practical reality of differences in soil, management history, landscape features, and micro-climate make it difficult to conclude that findings are the sole result of the tested treatments. To reduce uncertainty in studying diverse cropping systems while maintaining practical and scalar relevance, large and long-term experiments are needed, and likely new approaches to experimental design as well.

6. Conclusions

Here we explored the concept and implications of three-dimensional diversification of the arable field. We hypothesized that activating diversity in multiple dimensions at once would multiply the ecosystem service benefits, particularly of pest and disease regulation, and tested this hypothesis with two examples of strip and mixed intercropping in the Netherlands. Our results showed that spatial diversity alone was enough to increase biocontrol potential in wheat, whereas in the case of late blight in potato, the addition of genetic diversity within the strip did further improve disease mitigation. Based on these cases, we conclude that in-field crop diversity can enhance ecological regulation processes compared to monocultural systems, but that diversifying in multiple dimensions may not always be necessary depending on the targeted services. Compromises between complexity of management and the benefits of increased diversity are achievable, as is the case with strip cropping. This is interesting from a practical perspective, as strip cropping is already possible within current agronomic and mechanical constraints, requiring some adjustments to field conceptualization and management but not a full technological shift. If more positive response relationships are proven between stacked diversity dimensions and ecosystem service delivery, a move towards greater complexity (e.g. pixel cropping) could be a next step in the transition towards a more ecologically sound and productive model for redefining industrialized arable fields.

CRedit authorship contribution statement

Lenora Ditzler: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization. **Dirk F. van Apeldoorn:** . **Rogier P.O. Schulte:** Conceptualization, Writing - review & editing, Supervision. **Pablo Tittone:** Conceptualization, Writing - review & editing, Project administration. **Walter A.H. Rossing:** Conceptualization, Methodology, Writing - review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors report no declarations of interest.

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Janssen, Ambar Giovanna Hernández Romero, Yayang Vionita, and Yue Wang); and the anonymous reviewers whose feedback helped improve the paper.

Appendix A

A.1 Experiment layouts

Field Lab for Agroecology and Technology, Lelystad, NL
 Figs. A1, A2
 Droevendaal Experimental Farm, Wageningen, NL

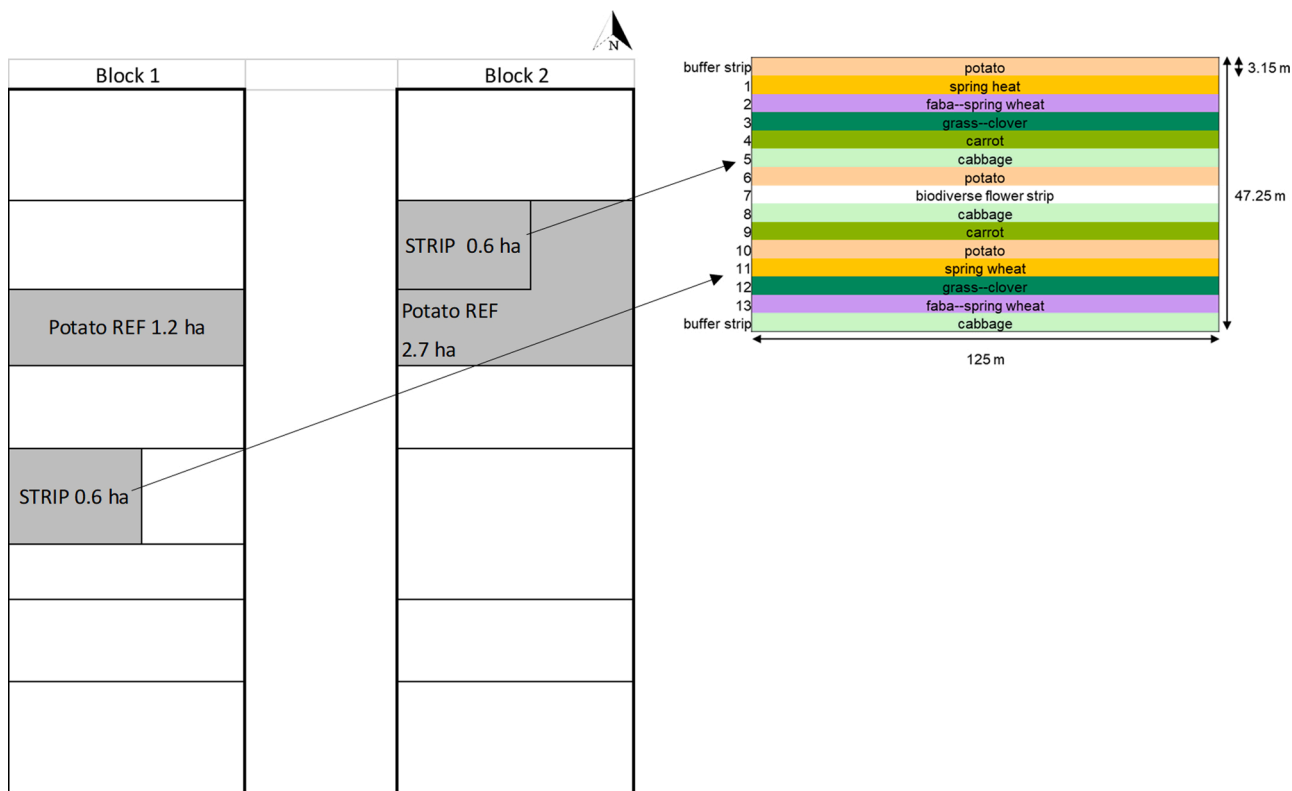


Fig. A1. Location of the strip and reference plots at the Field Lab for Agroecology and Technology in Lelystad (not to scale). Detail shows the strip arrangement within the STRIP treatment plot. Location of STRIP plots remained fixed throughout experiment years, REF plots rotated; map shows the layout in 2014.

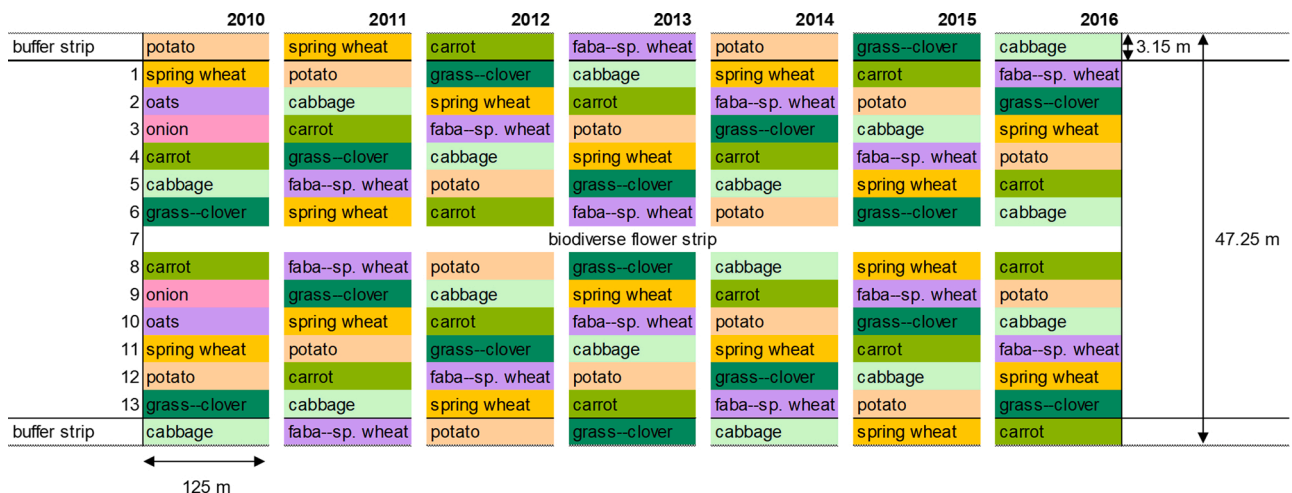


Fig. A2. Experimental layout and crop rotation in the strip treatments at the Field Lab for Agroecology and Technology in Lelystad, NL from 2010-2016 (not to scale). Schematic shows one experiment block; the full experiment consisted of two replicated blocks each following the same scheme.

Figs. A3, A4

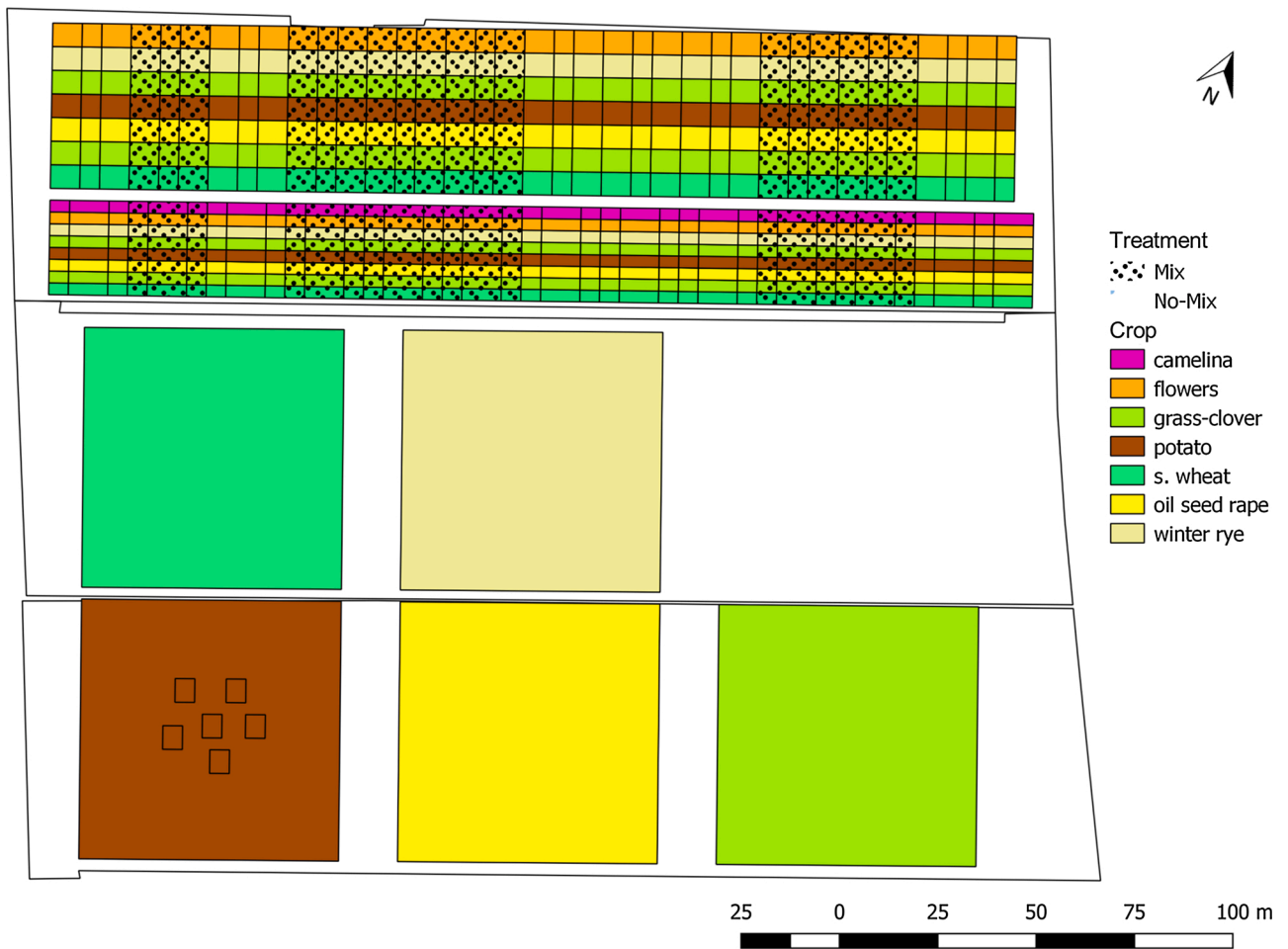


Fig. A3. Field layout of the strip cropping experiment located at Droevendaal Experimental Farm in Wageningen, The Netherlands. Map shows the crops sown in the 2017 growing season.

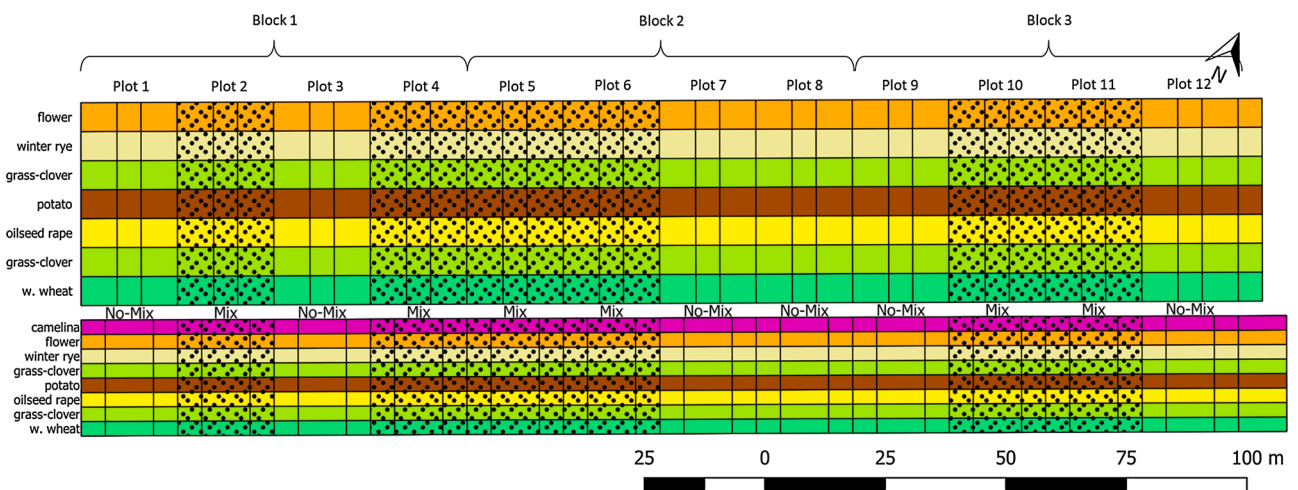


Fig. A4. Detailed layout of the strip treatments in the strip cropping experiment located at Droevendaal Experimental Farm in Wageningen, NL. Map shows the crops sown in the 2017 growing season.

A.2 Pitfall catches per natural enemy group

Fig. A5

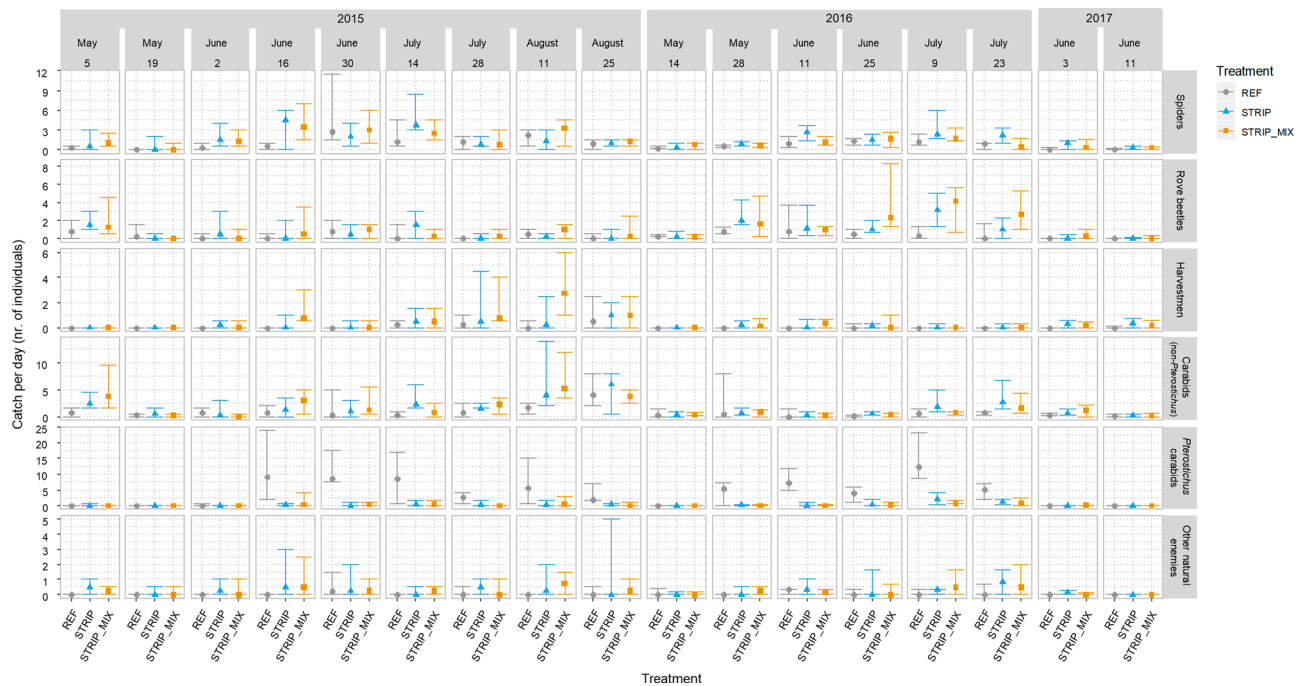


Fig. A5. Activity density (catch per day) of epigeic natural enemy groups in wheat collected by pitfall trapping in the three treatments (REF, grey circles; STRIP, blue triangles; STRIP_MIX, orange squares) at the Wageningen experiment from 2015–2017. Data are presented as clustered by date (medians aggregated across experiment blocks per date) to simplify the figure; in the statistical analysis data were clustered by observation date and experiment block. Points show median scores and bars show the range (minimum and maximum) in catches per cluster.

References

- Allema, B., van der Werf, W., Lenteren, J.C., Hemerik, L., Rossing, W.A.H., 2015. Movement behaviour of the carabid beetle *Pterostichus melanarius* in crops and at a habitat interface explains patterns of population redistribution in the field. *PLoS One* 9, e115751.
- Allema, B., Hemerik, L., Rossing, W.A.H., Groot, J.C.J., Lenteren, J.C., van der Werf, W., 2019. Dispersal of a carabid beetle in farmland is driven by habitat-specific motility and preference at habitat interfaces. *Entomol. Exp. Appl.* 167, 741–754. <https://doi.org/10.1111/eea.12804>.
- Andrivon, D., Lucas, J.-M., Ellissèche, D., 2003. Development of natural late blight epidemics in pure and mixed plots of potato cultivars with different levels of partial resistance. *Plant Pathol.* 52, 586–594. <https://doi.org/10.1046/j.1365-3059.2003.00882.x>.
- Barot, S., Allard, V., Cantarel, A., Enjalbert, J., Gauffreteau, A., Goldringer, I., Lata, J.-C., Le Roux, X., Niboyet, A., Porcher, E., 2017. Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. *Agron. Sustain. Dev.* 37, 13. <https://doi.org/10.1007/s13593-017-0418-x>.
- Bates, Douglas, Maechler, Martin, Bolker, Ben, Walker, Steve, 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Beillouin, D., Ben-Ari, T., Makowski, D., 2019. A dataset of meta-analyses on crop diversification at the global scale. *Data Brief* 24, 103898. <https://doi.org/10.1016/j.dib.2019.103898>.
- 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. R. Soc. B: Biol. Sci.* 273, 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>.
- Bommarco, Riccardo, Kleijn, David, Potts, Simon G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238. <https://doi.org/10.1016/j.tree.2012.10.012>.
- Bouws, H., Finckh, M.R., 2008. Effects of strip intercropping of potatoes with non-hosts on late blight severity and tuber yield in organic production. *Plant Pathol.* 57, 916–927. <https://doi.org/10.1111/j.1365-3059.2008.01860.x>.
- Brooker, Rob W., Bennett, Alison E., Cong, Wen-Feng, Daniell, Tim J., George, Timothy S., Hallett, Paul D., Hawes, Cathy, Iannetta, Pietro P.M., Jones, Hamlyn G., Karley, Alison J., Li, Long, McKenzie, Blair M., Pakeman, Robin J., Paterson, Eric, Schöb, Christian, Shen, Jianbo, Squire, Geoff, Watson, Christine A., Zhang, Chaochun, Zhang, Fusuo, Zhang, Junling, White, Philip J., 2015. Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. *New Phytol.* 206, 107–117. <https://doi.org/10.1111/nph.13132>.
- Bueren, Lammertsvan, Edith, T., Struik, Paul C., Eekeren, Nickvan, Nuijten, Edwin, 2018. Towards resilience through systems-based plant breeding. A review. *Agron. Sustain. Dev.* 38, 42. <https://doi.org/10.1007/s13593-018-0522-6>.
- Campbell, Bruce M., Beare, Douglas J., Bennett, Elena M., Hall-Spencer, Jason M., Ingram, John S.I., Jaramillo, Fernando, Ortiz, Rodomiro, Ramankutty, Navin, Sayer, Jeffrey A., Shindell, Drew, 2017. Agriculture production as a major driver of the Earth system exceeding planetary boundaries. *Ecol. Soc.* 22. <https://doi.org/10.5751/ES-09595-220408>.
- Caron, P., Bienabe, E., Hainzelin, E., 2014. Making transition towards ecological intensification of agriculture a reality: the gaps in and the role of scientific knowledge. *Curr. Opin. Environ. Sustain.* 8, 44–52. <https://doi.org/10.1016/j.cosust.2014.08.004>.
- Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., et al., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* 5. <https://doi.org/10.1126/sciadv.aax0121> eaax0121.
- Dassou, Anicet Gbèblonou, Tixier, Philippe, 2016. Response of pest control by generalist predators to local-scale plant diversity: a meta-analysis. *Ecol. Evol.* 6, 1143–1153. <https://doi.org/10.1002/ece3.1917>.
- De Minister van Landbouw, Natuurbeheer en Visserij, 2017. Regeling bestrijding schadelijke organismen, Article 8. Regeling bestrijding schadelijke organismen, Article 8: Overheid.nl. De Minister van Landbouw, Natuurbeheer en Visserij.
- Dedryver, Charles-Antoine, Le Ralec, Anne, Fabre, Frédéric, 2010. The conflicting relationships between aphids and men: a review of aphid damage and control strategies. *C. R. Biol.* 333, 539–553. <https://doi.org/10.1016/j.crv.2010.03.009>.
- Deutsch, Curtis A., Tewksbury, Joshua J., Tigchelaar, Michelle, Battisti, David S., Merrill, Scott C., Huey, Raymond B., Naylor, Rosamond L., 2018. Increase in crop losses to insect pests in a warming climate. *Science* 361, 916–919. <https://doi.org/10.1126/science.aat3466>.
- Dogliotti, S., Rossing, W.A.H., van Ittersum, M.K., 2003. ROTAT, a tool for systematically generating crop rotations. *Eur. J. Agron.* 19, 239–250. [https://doi.org/10.1016/S1161-0301\(02\)00047-3](https://doi.org/10.1016/S1161-0301(02)00047-3).
- Duru, Michel, Therond, Olivier, Fares, M. hand, 2015a. Designing agroecological transitions; A review. *Agron. Sustain. Dev.* 35, 1237–1257. <https://doi.org/10.1007/s13593-015-0318-x>.
- Duru, Michel, Therond, Olivier, Martin, Guillaume, Martin-Clouaire, Roger, Magne, Marie-Angéline, Justes, Eric, Journé, Etienne-Pascal, Aubertot, Jean-Noël, Savary, Serge, Bergez, Jacques-Eric, Sarthou, Jean Pierre, 2015b. How to implement biodiversity-based agriculture to enhance ecosystem services: a review. *Agron. Sustain. Dev.* 35, 1259–1281. <https://doi.org/10.1007/s13593-015-0306-1>.
- EPPO, 2008. *Phytophthora infestans* on potato. *Eppo Bull.* 38, 268–271. <https://doi.org/10.1111/j.1365-2338.2008.01224.x>.

- Eurostat, 2018. Main Annual Crop Statistics. In *Main Annual Crop Statistics*: Eurostat.
- Fahrig, Lenore, Girard, Judith, Duro, Dennis, Pasher, Jon, Smith, Adam, Javorek, Steve, King, Douglas, Lindsay, Kathryn, Freemark, Mitchell, Scott, Tischendorf, Lutz, 2015. Farmlands with smaller crop fields have higher within-field biodiversity. *Agric. Ecosyst. Environ.* 200, 219–234. <https://doi.org/10.1016/j.agee.2014.11.018>.
- Foley, Jonathan A., DeFries, Ruth, Asner, Gregory P., Barford, Carol, Bonan, Gordon, Carpenter, Stephen R., Stuart Chapin, F., Coe, Michael T., Daily, Gretchen C., Gibbs, Holly K., Helkowski, Joseph H., Holloway, Tracey, Howard, Erica A., Kucharik, Christopher J., Monfreda, Chad, Patz, Jonathan A., Colin Prentice, I., Ramankutty, Navin, Snyder, PeterK., 2005. Global consequences of land use. *Science* 309, 570–574. <https://doi.org/10.1126/science.1111772>.
- Geertsema, Willemien, Rossing, Walter A.H., Landis, Douglas A., Bianchi, Felix J.J.A., Rijn, Paul C.J., Schaminée, Joop H.J., Tschamtkte, Teja, van der Werf, Wopke, 2016. Actionable knowledge for ecological intensification of agriculture. *Front. Ecol. Environ.* 14, 209–216. <https://doi.org/10.1002/fee.1258>.
- Groot, Jeroen C.J., Rossing, Walter A.H., 2011. Model-aided learning for adaptive management of natural resources: an evolutionary design perspective. *Methods Ecol. Evol.* 2, 643–650. <https://doi.org/10.1111/j.2041-210X.2011.00114.x>.
- Groot, Jeroen C.J., Jellema, André, Rossing, Walter A.H., 2010. Designing a hedgerow network in a multifunctional agricultural landscape: Balancing trade-offs among ecological quality, landscape character and implementation costs. *Eur. J. Agron.* 32, 112–119. <https://doi.org/10.1016/j.eja.2009.07.002>.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, e1500052 <https://doi.org/10.1126/sciadv.1500052>.
- Hatt, Séverin, Lopes, Thomas, Boeraeve, Fanny, Chen, Julian, Francis, Frédéric, 2017. Pest regulation and support of natural enemies in agriculture: experimental evidence of within field wildflower strips. *Ecol. Eng.* 98, 240–245. <https://doi.org/10.1016/j.ecoleng.2016.10.080>.
- Hatt, Séverin, Boeraeve, Fanny, Artru, Sidonie, Dufrière, Marc, Francis, Frédéric, 2018. Spatial diversification of agroecosystems to enhance biological control and other regulating services: an agroecological perspective. *Sci. Total Environ.* 621, 600–611. <https://doi.org/10.1016/j.scitotenv.2017.11.296>.
- Haugaard-Nielsen, Henrik, Jørgensen, Bjarne, Kinane, Julia, Jensen, Erik Steen, 2008. Grain legume–cereal intercropping: the practical application of diversity, competition and facilitation in arable and organic cropping systems. *Renew. Agric. Food Syst.* 23, 3–12. <https://doi.org/10.1017/s1742170507002025>.
- Haverkort, A.J., Boonekamp, P.M., Hutten, R., Jacobsen, E., Lotz, L.A.P., Kessel, G.J.T., Visser, R.G.F., van der Vossen, E.A.G., 2008. Societal costs of late blight in potato and prospects of durable resistance through cisgenic modification. *Potato Res.* 51, 47–57. <https://doi.org/10.1007/s11540-008-9089-y>.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Höglberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127. <https://doi.org/10.1126/science.286.5442.1123>.
- Hothorn, Torsten, Bretz, Frank, Westfall, Peter, 2008. Simultaneous inference in general parametric models. *Biom. J.* 50, 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Hufnagel, Johannes, Reckling, Moritz, Ewert, Frank, 2020. Diverse approaches to crop diversification in agricultural research. A review. *Agron. Sustain. Dev.* 40, 1–17. <https://doi.org/10.1007/s13593-020-00617-4>.
- Isbell, Forest, Adler, Paul R., Eisenhauer, Nico, Fornara, Dario, Kimmel, Kaitlin, Kremen, Claire, Letourneau, Deborah K., Liebman, Matt, Wayne Polley, H., Quijas, Sandra, Scherer-Lorenzen, Michael, 2017. Benefits of increasing plant diversity in sustainable agroecosystems. *J. Ecol.* 105, 871–879. <https://doi.org/10.1111/1365-2745.12789>.
- Iverson, Aaron L., Marín, Linda E., Ennis, Katherine K., Gonthier, David J., Connor-Barrie, Benjamin T., Remfert, Jane L., Cardinale, Bradley J., Perfecto, Ivette, 2014. Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. *J. Appl. Ecol.* 51, 1593–1602. <https://doi.org/10.1111/1365-2664.12334>.
- Jepsen, Martin Rudbeck, Kuemmerle, Tobias, Müller, Daniel, Erb, Karlheinz, Verburg, Peter H., Haberl, Helmut, Vesterager, Jens Peter, Andrić, Maja, Antrop, Marc, Austrheim, Gunnar, Björn, Ismo, Bondeau, Alberte, Bürgi, Matthias, Bryson, Jessica, Caspar, Gilles, Cassar, Louis F., Conrad, Elisabeth, Chromý, Pavel, Daugirdas, Vidmantas, Eetvelde, Veerle Van, Elena-Rosselló, Ramon, Gimmi, Urs, Izakovicova, Zita, Jancák, Vít, Jansson, Ulf, Kladnik, Drago, Kozak, Jacek, Konkoly-Gyuró, Eva, Krausmann, Fridolin, Mander, Úlo, McDonagh, John, Pärn, Jaan, Niedertscheider, Maria, Nikodemus, Olgerts, Ostapowicz, Katarzyna, Pérez-Soba, Marta, Pinto-Correia, Teresa, Ribokas, Gintaras, Rounsevell, Mark, Schistou, Despoina, Schmit, Claude, Terkenli, Theano S., Tretvik, Aud M., Trzepak, Piotr, Vadineanu, Angheluta, Walz, Ariane, Zhllima, Edvin, Reenberg, Anette, 2015. Transitions in European land-management regimes between 1800 and 2010. *Land Use Policy* 49, 53–64. <https://doi.org/10.1016/j.landusepol.2015.07.003>.
- Jiang, Yujing, 2018. Clusrank: Wilcoxon Rank Sum Test for Clustered Data. [clusrank: Wilcoxon Rank Sum Test for Clustered Data](https://www.r-project.org/web/packages/clusrank/index.html).
- Kinzig, Ann P., Ryan, Phil A., Etienne, Michel, Allison, Helen E., Elmqvist, Thomas, Walker, Brian H., 2006. Resilience and regime shifts: assessing cascading effects. *Ecol. Soc.* 11.
- Kremen, Claire, Miles, Albie, 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecol. Soc.* 17 <https://doi.org/10.5751/ES-05035-170440>.
- Kremen, Claire, Iles, Alastair, Bacon, Christopher, 2012. Diversified farming systems: an agroecological, systems-based alternative to modern industrial agriculture. *Ecol. Soc.* 17 <https://doi.org/10.5751/ES-05103-170444>.
- Lammerts van Bueren, E.T., Tiemens-Hulscher, M., Struijk, P.C., 2008. Cisgenesis does not solve the late blight problem of organic potato production: alternative breeding strategies. *Potato Res.* 51, 89. <https://doi.org/10.1007/s11540-008-9092-3>.
- Leoni, Carolina, Rossing, Walter, Bruggen, Ariena H.Cvan, 2015. Crop rotation. In: Finckh, M.R., van Bruggen, A.H.C., Tamm, L. (Eds.), *Plant Diseases and Their Management in Organic Agriculture*. APS Press.
- Letourneau, Deborah K., Armbrrecht, Inge, Rivera, Beatriz Salguero, Lerma, James Montoya, Carmona, Elizabeth Jiménez, Daza, Martha Constanza, Escobar, Selene, Galindo, Víctor, Gutiérrez, Catalina, López, Sebastián Duque, Mejía, Jessica López, Rangel, Aleyda Maritza Acosta, Ranges, Janine Herrera, Rivera, Leonardo, Saavedra, Carlos Arturo, Torres, Alba Marina, Trujillo, Aldemar Reyes, 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21, 9–21. <https://doi.org/10.1890/09-2026.1>.
- Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batary, P., Berendse, F., Bommarco, R., Bosque-Perez, N.A., Carvalho, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Astrom, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Poccock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlof, M., Sardinias, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tschamtkte, T., Vesely, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob. Chang. Biol.* 23, 4946–4957. <https://doi.org/10.1111/gcb.13714>.
- Lopes, T., Bodson, B., Francis, F., 2015. Associations of wheat with pea can reduce Aphid infestations. *Neotrop. Entomol.* 44, 286–293. <https://doi.org/10.1007/s13744-015-0282-9>.
- Lopes, Thomas, Hatt, Séverin, Xu, Qinxuan, Chen, Julian, Liu, Yong, Francis, Frédéric, 2016. Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control. *Pest Manag. Sci.* 72, 2193–2202. <https://doi.org/10.1002/ps.4332>.
- Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *BioScience* 56, 311–323. [https://doi.org/10.1641/0006-3568\(2006\)56\[311:Tevoes\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2006)56[311:Tevoes]2.0.Co;2).
- Madden, Laurence V., Hughes, Gareth, Bosch, Frankvanden, 2007. *The Study of Plant Disease Epidemics*. APS Press, St. Paul, Minnesota.
- Magrini, Marie-Benoît, Anton, Marc, Cholez, C.élie, Corre-Hellou, Guenaelle, Duc, G.é rard, Jeuffroy, Marie-H.é lène, Meynard, Jean-Marc, Pelzer, Elise, Voisin, Anne-Sophie, Walrand, Stéphane, 2016. Why are grain-legumes rarely present in cropping systems despite their environmental and nutritional benefits? Analyzing lock-in in the French agrifood system. *Ecol. Econ.* 126, 152–162. <https://doi.org/10.1016/j.ecolecon.2016.03.024>.
- Malézieux, Eric, 2012. Designing cropping systems from nature. *Agron. Sustain. Dev.* 32, 15–29. <https://doi.org/10.1007/s13593-011-0027-z>.
- Martin, Emily A., Dainese, Matteo, Clough, Yann, Báldi, András, Bommarco, Riccardo, Gagic, Vesna, Garratt, Michael P.D., Holzschuh, Andrea, Kleijn, David, Kovács-Hostyánszki, Anikó, Marini, Lorenzo, Potts, Simon G., Smith, Henrik G., Hassan, Diab Al, Albrecht, Matthias, Andersson, Georg K.S., Asís, Josep D., Aviron, Stéphanie, Balzan, Mario V., Baños-Picón, Laura, Bartomeus, Ignasi, Batáry, P.éter, Burel, Françoise, Caballero-López, Berta, Concepción, Elena D., Coudran, Valérie, Dänhardt, Juliana, Diaz, Mario, Diekötter, Tim, Dormann, Carsten F., Dufloy, R.é mi, Entling, Martin H., Farwig, Nina, Fischer, Christina, Frank, Thomas, Garibaldi, Lucas A., Hermann, John, Herzog, Felix, Inclán, Diego, Jacot, Katja, Jauker, Frank, Jeanneret, Philippe, Kaiser, Marina, Krauss, Jochen, Féon, Violette Le, Marshall, Jon, Moonen, Anna-Camilla, Moreno, Gerardo, Riedinger, Verena, Rundlöf, Maj, Rusch, Adrien, Scheper, Jeroen, Schneider, Gudrun, Schüepp, Christof, Stutz, Sonja, Sutter, Louis, Tamburini, Giovanni, Thies, Carsten, Tormos, José, Tschamtkte, Teja, Tschumi, Matthias, Uzman, Deniz, Wagner, Christian, Zubair-Anjum, Muhammad, Steffan-Dewenter, Ingolf, 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecol. Lett.* 22, 1083–1094. <https://doi.org/10.1111/ele.13265>.
- Mawois, Marie, Vidal, Andréa, Revoyron, Eva, Casagrande, Marion, Jeuffroy, Marie-H.é lène, Le Bail, Marianne, 2019. Transition to legume-based farming systems requires stable outlets, learning, and peer-networking. *Agron. Sustain. Dev.* 39, 14. <https://doi.org/10.1007/s13593-019-0559-1>.
- Meynard, Jean-Marc, Charrier, François, Fares, M. hand, Le Bail, Marianne, Magrini, Marie-Benoît, Charlier, Aude, Messéan, Antoine, 2018. Socio-technical lock-in hinders crop diversification in France. *Agron. Sustain. Dev.* 38, 54. <https://doi.org/10.1007/s13593-018-0535-1>.
- Möller, Kurt, Habermeyer, Johann, Zinkernagel, Volker, Reents, Hans-Jürgen, 2006. Impact and interaction of nitrogen and Phytosphora infestans as yield-limiting and yield-reducing factors in organic potato (*Solanum tuberosum* L.) crops. *Potato Res.* 49, 281–301. <https://doi.org/10.1007/s11540-007-9024-7>.

- Morel, Kevin, Revoyron, Eva, Cristobal, Magali San, Baret, Philippe V., 2020. Innovating within or outside dominant food systems? Different challenges for contrasting crop diversification strategies in Europe. *PLoS One* 15, e0229910. <https://doi.org/10.1371/journal.pone.0229910>.
- Oksanen, Jari, Guillaume Blanchet, F., Friendly, Michael, Kindt, Roeland, Legendre, Pierre, McGlenn, Dan, Minchin, Peter R., O'Hara, R.B., Simpson, Gavin L., Solymos, Peter, Stevens, M.Henry H., Szocs, Eduard, Wagner, Helene, 2019. *Vegan: Community ecology package*. *vegan: Community Ecology Package*.
- Pacilly, Francine C.A., Hofstede, Gert Jan, Bueren, Edith T.Lammertsvan, Kessel, Geert J. T., Groot, Jeroen C.J., 2018. Simulating crop-disease interactions in agricultural landscapes to analyse the effectiveness of host resistance in disease control: the case of potato late blight. *Ecol. Modell.* 378, 1–12. <https://doi.org/10.1016/j.ecolmodel.2018.03.010>.
- Pacilly, Francine C.A., Edith, T., Bueren, Lammertsvan, Groot, Jeroen C.J., Hofstede, Gert Jan, 2019. Moving perceptions on potato late blight control: workshops with model-based scenarios. *Crop. Prot.* 119, 76–87. <https://doi.org/10.1016/j.cropro.2019.01.010>.
- Patzek, Tad W., 2008. Thermodynamics of agricultural sustainability: the case of US maize agriculture. *Crit. Rev. Plant Sci.* 27, 272–293. <https://doi.org/10.1080/07352680802247971>.
- Pelzer, Elise, Bazot, Mathieu, Makowski, David, Corre-Hellou, Guénaëlle, Naudin, Christophe, Rifai, Mehdi Al, Baranger, Edouard, Bedoussac, Laurent, Biarnès, V.éronique, Boucheny, Patrick, Carrouée, Benoit, Dorvillez, Daniel, Foissy, Damien, Gaillard, Bernard, Guichard, Laurence, Mansard, Marie-Chantal, Omon, Bertrand, Prieur, Loïc, Yvergniaux, Morgane, Justes, Eric, Jeuffroy, Marie-H.é lène, 2012. Pea-wheat intercrops in low-input conditions combine high economic performances and low environmental impacts. *Eur. J. Agron.* 40, 39–53. <https://doi.org/10.1016/j.eja.2012.01.010>.
- Pelzer, Elise, Modotti, Martina, Ballot, Remy, Jeuffroy, M.H., 2019. Motivations and observed benefits and limits from farmers growing legumes. In: *Motivations and Observed Benefits and Limits from Farmers Growing Legumes*, European Conference on Crop Diversification. Budapest, Hungary: Zenodo.
- Poveda, K., Gomez, M.I., Martinez, E., 2008. Diversification practices: their effect on pest regulation and production. *Revista Colombiana de Entomologia* 34, 131–144.
- Ratnadass, Alain, Fernandes, Paula, Avelino, Jacques, Habib, Robert, 2012. Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review. *Agron. Sustain. Dev.* 32, 273–303. <https://doi.org/10.1007/s13593-011-0022-4>.
- Reckling, Moritz, Döring, Thomas F., Bergkvist, G.öran, Stoddard, Frederick L., Watson, Christine A., Seddig, Sylvia, Chmielewski, Frank-M., Bachinger, Johann, 2018. Grain legume yields are as stable as other spring crops in long-term experiments across northern Europe. *Agron. Sustain. Dev.* 38, 63. <https://doi.org/10.1007/s13593-018-0541-3>.
- Renard, Delphine, Tilman, David, 2019. National food production stabilized by crop diversity. *Nature* 571, 257–260. <https://doi.org/10.1038/s41586-019-1316-y>.
- Robertson, G., Philip, K.L., Gross, S.K., Hamilton, D.A.Landis, Schmidt, T.M., Snapp, S.S., Swinton, S.M., 2014. Farming for ecosystem services: an ecological approach to production agriculture. *BioScience* 64, 404–415. <https://doi.org/10.1093/biosci/biu037>.
- Roesch-McNally, Gabrielle E., Ar Buckley, J.G., Tyndall, John C., 2018. Barriers to implementing climate resilient agricultural strategies: the case of crop diversification in the U.S. Corn Belt. *Glob. Environ. Chang. Part A* 48, 206–215. <https://doi.org/10.1016/j.gloenvcha.2017.12.002>.
- Root, Richard B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43, 95–124. <https://doi.org/10.2307/1942161>.
- Rosa-Schleich, Julia, Loos, Jacqueline, Mußhoff, Oliver, Tscharnkte, Teja, 2019. Ecological-economic trade-offs of diversified farming systems – a review. *Ecol. Econ.* 160, 251–263. <https://doi.org/10.1016/j.ecolecon.2019.03.002>.
- Schmidt, Martin H., Lauer, Andreas, Purtauf, Tobias, Thies, Carsten, Schaefer, Matthias, Tscharnkte, Teja, 2003. Relative importance of predators and parasitoids for cereal aphid control. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 1905–1909. <https://doi.org/10.1098/rspb.2003.2469>.
- Sirami, Clélia, Gross, Nicolas, Baillod, Alette Bøsem, Bertrand, Colette, Carrié, Romain, Hass, Annika, Henckel, Laura, Miguët, Paul, Vuillot, Carole, Alignier, Audrey, Girard, Jude, Batáry, P.éter, Clough, Yann, Violle, Cyrille, Giralt, David, Bota, Gerard, Badenhauer, Isabelle, Lefebvre, Gaëtan, Gauffre, Bertrand, Vialatte, Aude, Calatayud, François, Gil-Tena, Assu, Tischendorf, Lutz, Mitchell, Scott, Lindsay, Kathryn, Georges, Romain, Hilaire, Samuel, Recasens, Jordi, Solé-Senan, Xavier Oriol, Robleño, Irene, Bosch, Jordi, Barrientos, Jose Antonio, Ricarte, Antonio, Marcos-García, MaríaÁngeles, Miñano, Jesús, Mathevet, Raphaël, Gibon, Annick, Baudry, Jacques, Balent, G.érard, Poulin, Brigitte, Burel, Françoise, Tscharnkte, Teja, Bretagnolle, Vincent, Siriwardena, Gavin, Ouin, Annie, Brotons, Luis, Martin, Jean-Louis, Fahrig, Lenore, 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci.* 116, 16442–16447. <https://doi.org/10.1073/pnas.1906419116>.
- Skal, 2020. *EC Legislation. Skal Bio Controle, The Netherlands*.
- Skelsey, P., Rossing, W.A.H., Kessel, G.J.T., Powell, J., van der Werf, W., 2005. Influence of host diversity on development of epidemics: an evaluation and elaboration of mixture theory. *Phytopathology* 95, 328–338. <https://doi.org/10.1094/phyto-95-0328>.
- Skelsey, P., Kessel, G.J.T., Rossing, W.A.H., van der Werf, W., 2009. Parameterization and evaluation of a spatiotemporal model of the potato late blight pathosystem. *Phytopathology* 99, 290–300. <https://doi.org/10.1094/phyto-99-3-0290>.
- Skelsey, P., Rossing, W.A.H., Kessel, G.J.T., Werf, W., 2010. Invasion of *Phytophthora infestans* at the landscape level: how do spatial scale and weather modulate the consequences of spatial heterogeneity in host resistance? *Phytopathology* 100, 1146–1161. <https://doi.org/10.1094/phyto-06-09-0148>.
- Snyder, William E., Ives, Anthony R., 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* 84, 91–107. [https://doi.org/10.1890/0012-9658\(2003\)084\[0091:IBSAGN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0091:IBSAGN]2.0.CO;2).
- Steingröver, Eveliene G., Geertsema, Willemien, van Wingerden, Walter K.R.E., 2010. Designing agricultural landscapes for natural pest control: a transdisciplinary approach in the Hoeksche Waard (the Netherlands). *Landscape Ecol.* 25, 825–838. <https://doi.org/10.1007/s10980-010-9489-7>.
- Storkey, Jonathan, Döring, Thomas, Baddeley, John, Collins, Rosemary, Roderick, Stephen, Jones, Hannah, Watson, Christine, 2015. Engineering a plant community to deliver multiple ecosystem services. *Ecol. Appl.* 25, 1034–1043. <https://doi.org/10.1890/14-1605.1>.
- Tajmiri, Pejman, Fathi, Seyed Ali Asghar, Golizadeh, Ali, Nouri-Ganbalani, Gadir, 2017. Effect of strip-intercropping potato and annual alfalfa on populations of *Leptinotarsa decemlineata* say and its predators. *Int. J. Pest Manag.* 63, 273–279. <https://doi.org/10.1080/09670874.2016.1256513>.
- Tatchell, G.M., 1989. An estimate of the potential economic losses to some crops due to aphids in Britain. *Crop. Prot.* 8, 25–29. [https://doi.org/10.1016/0261-2194\(89\)90095-1](https://doi.org/10.1016/0261-2194(89)90095-1).
- Team, R.Core, 2018. *R: A Language and Environment for Statistical Computing*. In: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Thomas, C.F.G., Brown, N.J., Kendall, D.A., 2006. Carabid movement and vegetation density: implications for interpreting pitfall trap data from split-field trials. *Agric. Ecosyst. Environ.* 113, 51–61. <https://doi.org/10.1016/j.agee.2005.08.033>.
- Tilman, David, Reich, Peter B., Knops, Johannes, Wedin, David, Mielke, Troy, Lehman, Clarence, 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–845. <https://doi.org/10.1126/science.1060391>.
- Tilman, David, Balzer, Christian, Hill, Jason, Befort, Belinda L., 2011. Global food demand and the sustainable intensification of agriculture. *PNAS* 108, 20260–20264. <https://doi.org/10.1073/pnas.1116437108>.
- Tittonell, Pablo, Klerkx, Laurens, Baudron, Frédéric, Félix, Georges F., Ruggia, Andrea, Apeldoorn, Dirkvan, Dogliotti, Santiago, Mapfumo, Paul, Rossing, Walter A.H., 2016. In: Lichtfouse, Eric (Ed.), *Ecological Intensification: Local Innovation to Address Global Challenges*. In *Sustainable Agriculture Reviews*, vol. 19. Cham: Springer International Publishing, pp. 1–34.
- Van Apeldoorn, Dirk F., Kok, Kasper, Sonneveld, Marthijn P.W., Veldkamp, A., 2011. *Panarchy rules: rethinking resilience of agroecosystems, evidence from Dutch dairy farming*. *Ecol. Soc.* 16, -.
- van der Zanden, Emma H., Levers, Christian, Verburg, Peter H., Kuemmerle, Tobias, 2016. Representing composition, spatial structure and management intensity of European agricultural landscapes: a new typology. *Landscape Urban Plan.* 150, 36–49. <https://doi.org/10.1016/j.landurbplan.2016.02.005>.
- van Oort, P.A.J., Gou, F., Stomph, T.J., van der Werf, W., 2020. Effects of strip width on yields in relay-strip intercropping: a simulation study. *Eur. J. Agron.* 112, 125936. <https://doi.org/10.1016/j.eja.2019.125936>.
- van Vliet, Jasper, de Groot, Henri L.F., Rietveld, Piet, Verburg, Peter H., 2015. Manifestations and underlying drivers of agricultural land use change in Europe. *Landscape Urban Plan.* 133, 24–36. <https://doi.org/10.1016/j.landurbplan.2014.09.001>.
- Vanloqueren, Gaëtan, Baret, Philippe V., 2009. How agricultural research systems shape a technological regime that develops genetic engineering but locks out agroecological innovations. *Res. Policy* 38, 971–983. <https://doi.org/10.1016/j.respol.2009.02.008>.
- Venter, Zander Samuel, Jacobs, Karin, Hawkins, Heidi-Jayne, 2016. The impact of crop rotation on soil microbial diversity: a meta-analysis. *Pedobiologia* 59, 215–223. <https://doi.org/10.1016/j.pedobi.2016.04.001>.
- Weisberger, David, Nichols, Virginia, Liebman, Matt, 2019. Does diversifying crop rotations suppress weeds? A meta-analysis. *PLoS One* 14, e0219847. <https://doi.org/10.1371/journal.pone.0219847>.
- Wezel, Alexander, Casagrande, Marion, Celette, Florian, Vian, Jean-François, Ferrer, Aurélie, Peigné, Joséphine, 2014. Agroecological practices for sustainable agriculture. A review. *Agron. Sustain. Dev.* 34, 1–20. <https://doi.org/10.1007/s13593-013-0180-7>.
- Yu, Yang, Stomph, Tjeerd-Jan, Makowski, David, van der Werf, Wopke, 2015. Temporal niche differentiation increases the land equivalent ratio of annual intercrops: a meta-analysis. *Field Crops Res.* 184, 133–144. <https://doi.org/10.1016/j.fcr.2015.09.010>.
- Zhang, Chaochun, Dong, Yan, Tang, Li, Zheng, Yi, Makowski, David, Yu, Yang, Zhang, Fusuo, van der Werf, Wopke, 2019. Intercropping cereals with faba bean reduces plant disease incidence regardless of fertilizer input; a meta-analysis. *Eur. J. Plant Pathol.* <https://doi.org/10.1007/s10658-019-01711-4>.
- Zhu, Youyong, Chen, Hairu, Fan, Jinghua, Wang, Yunyue, Li, Yan, Chen, Jianbing, Fan, Jin Xiang, Yang, Shisheng, Hu, Lingping, Leung, Hei, Mew, Tom W., Teng, Paul S., Wang, Zonghua, Mundt, Christopher C., 2000. Genetic diversity and disease control in rice. *Nature* 406, 718. <https://doi.org/10.1038/35021046>.
- Zuur, Alain, Ieno, Elena N., Walker, Neil, Saveliev, Anatoly A., Smith, Graham M., 2009. *Mixed Effects Models and Extensions in Ecology With R*: Springer Science & Business Media.