Agriculture Communications 1 (2023) 100004

Contents lists available at ScienceDirect

Agriculture Communications

journal homepage: www.sciencedirect.com/journal/agriculture-communications

Crop diversification to promote arthropod pest management: A review

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ARTICLE INFO

Keywords:
Biocontrol
Insect
Integrated pest management (IPM)
Pest pressure
Spatial scale

ABSTRACT

Agricultural intensification has led to a drastic simplification and homogenization of agroecosystems, causing biodiversity loss and an increased reliance on chemical pesticides to control arthropod crop pests. However, these pesticides have major negative impacts on biodiversity, ecosystem services, and human health. Restoring plant diversity in agricultural landscapes could revert this trend, promote biological pest control and reduce the reliance on chemical insecticides. Crop diversification is especially useful to promote populations of pests' natural enemies and reduce pest densities, since it does not require a reduction in cropped areas compared to set-aside strategies based on non-crop habitats. We review recent advances on the benefits of crop diversification for arthropod pest control and cover the important ecological mechanisms, tools and scales to implement crop diversification. We also compare the relative benefits of crop and non-crop diversification strategies based on estimates from published meta-analyses. Finally, we summarise the benefits of crop diversification beyond biological control, and highlight the main constraints currently preventing wider implementation to guide future research directions.

1. Introduction

Agricultural intensification has led to a drastic simplification of agroecosystems, especially in terms of crop diversity [1]. 0.4% of edible plants are grown for human food, with nine species – wheat, barley, sorgho/millet, potato, sweet potato/yam, sugar cane, and soybean – representing more than 75% of human energy requirements at a global scale [2]. Low crop diversity, particularly at the varietal level, is further constrained by patents on seed production, which protect seed companies but prevent farmers from growing their own seeds issued from varieties under patents [2].

Arthropod pests are responsible for major yield losses worldwide: from 2001 to 2003, yield losses due to pest damage reached 28% in wheat and cotton, 26% in soybean, 37% in rice, 31% in maize, and 40% in potato [3]. Arthropod pest control heavily relies on synthetic chemical insecticides worldwide, which have major negative impacts on the environment and on human health; they are detrimental to non-target organisms and induce pest resistances, further increasing farmers' dependency on chemical insecticides [4–6].

Biological pest control is the top-down regulation of crop pests by natural enemies through predation or parasitism. It is an important alternative to chemical pest control to prevent pest outbreaks and limit pest densities, and a key component of integrated pest management (IPM) [7]. Biological pest control services are destabilized by intensive farming, through landscape simplification and the massive use of chemical insecticides and mineral fertilisers. Chemical insecticides directly reduce the abundance and diversity of natural enemies in agroecosystems, while mineral fertilisers stimulate crop plants growth and increase their sensitivity to pests, leading to pest outbreaks [6,8]. Landscape simplification, through the reduction and fragmentation of semi-natural habitats, the large field sizes, and the use of low crop diversity, reduces habitat diversity, and therefore the natural enemy pool [9,10].

Maintaining a high functional diversity of natural enemies increases biological control efficacy [11]. Diverse natural enemy communities can be promoted through the provision of diverse food resources (e.g., diversity of prey/host species, floral resources) and habitats providing shelter [12,13]. This is the essence of conservation biological control, which seeks to promote biological control services provided by pests' natural enemies that are naturally present in agroecosystems through habitat management [13]. Such habitat management relies on the manipulation of plant and habitat diversity to enhance natural enemies

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https://doi.org/10.1016/j.agrcom.2023.100004
Received 27 February 2023; Received in revised form 30 May 2023; Accepted 31 May 2023
Available online 22 June 2023

and reduce pest pressure [13]. Diversification can be deployed across different spatial scales (from field to landscape to the supply chain), which are interconnected [14,15].

It is now well demonstrated that maintaining semi-natural habitats, such as forests or grasslands, is a key strategy to support a large and diverse pool of natural enemy species, and to strengthen biological pest control in agricultural landscapes [16,17], although there are limitations [18]. Despite this large body of knowledge, such strategy based on non-crop habitats management is rarely implemented by farmers [19]. Enhancing biological pest control through crop diversification could be a more appealing yet efficient alternative to non-crop habitat diversification to enhance biological pest control services [18], since it does not require set-aside agricultural land from production [20,21]. However, we lack a comprehensive overview of the potential benefits of crop diversification strategies for pest management in agricultural landscapes.

Here, we first outline the main ecological processes by which crop diversification promotes pest regulation, either directly (bottom-up effects) or indirectly (top-down effects by natural enemies controlling pest populations). We then review the main crop diversification strategies available across spatio-temporal scales, based on a review of the recent literature (Table 1). We focus on above-ground arthropod pests, due to their economic impacts and the importance of ecological processes as potential regulation strategies [3,22]. Taking advantage of recent relevant meta-analyses, we attempt to estimate the relative contributions of crop diversification versus non-crop habitat diversification strategies on pest management (Fig. 1; Table 2). In this sense, this literature review does not aim to be systematic, but instead provides a broad overview on the available diversification practices that have been evaluated for their efficacy. Finally, we briefly summarize the benefits of crop diversification beyond biological pest control, and the barriers to the adoption of crop diversification measures.

2. Ecological processes by which crop diversity promotes pest regulation

Creating agroecosystems that reduce crop pest pressure relies on bottom-up effects reducing the conditions that favour pests, and top-down effects promoting the biological control of pest populations by natural enemies. Although many of the underlying mechanisms reviewed below have been described and are presented in the context of natural biological control, they can similarly promote crop pests' natural enemies introduced as biocontrol agents in augmentative biocontrol strategies, notably by facilitating their population establishment and growth [23]. Crop diversification can directly and indirectly reduce pest populations through the resource concentration hypothesis and the natural enemy hypothesis, respectively [24]. In this section, we present these hypotheses and review the main mechanisms by which crop diversification can promote pest regulation.

2.1. Bottom-up effects: reducing pest population establishment

Bottom-up effects on arthropod herbivorous crop pests are mediated by the abiotic environment or by the primary trophic level [24]. Crop diversification over space and time can directly limit pest populations through three main types of bottom-up effects: (i) altering the detection and selection of the main host crop plant by arthropod pests; (ii) enhancing crop resistance or tolerance to pests, and (iii) breaking resource spatio-temporal continuity. The magnitude and relative importance of these effects highly depend on the target pests' functional traits such as dispersal abilities and diet breadth, and we yet lack comprehensive studies analysing their respective importance in a diversity of agricultural contexts. We nonetheless review those three main mechanisms below.

Crop diversification can strongly impact pests' abilities to detect and select their host plant or host patches. Arthropod pests use visual and chemical signals specific to their host crop plant to locate and select the best patches, and increasing crop diversity within-field or at the landscape scale can confuse these signals [25]. A large number of arthropod pests use crop visual cues to detect and select their host plant [26]. For instance, aphids select their host plant based on its colour, determining its nutritional status [27], while changes in visual signals of virus-infected host plants affect host selection by whiteflies [28]. The use of a variety of visual host crop plant signals (size, architecture, colour) are modulated by the distance and by arthropod pest requirements (food source, oviposition site), and may therefore be affected by crop diversification over various spatial scales [29]. In addition to visual signals, olfactory signals made of volatile organic compounds (VOCs) emitted by crop plants play a major role in the detection of the host crop plant by arthropod pests [30,31]. Since each crop species and even each crop variety has a unique olfactive signature, increasing crop diversity will mix and dilute the corresponding specific signatures, confusing the detection of host crop plants by pests [32]. Such approach is the basis for a number of crop-diversification-based pest control strategies, including intercropping and push–pull systems (reviewed in section 3.1.).

As discussed above, crop nutritional quality is an important driver of crop pests' host preferences, but also of their population growth, since the nutritional quality directly affects individual fitness [24]. Mixtures of diverse varieties of the same crop (cultivars) varying the nutritional quality of the associated varieties could reduce the build-up of specialist pest populations [33]. Crop diversification can also enhance crop defences against pests attacks, which are usually classified under resistance or tolerance strategies [34]. Resistance traits typically prevent or reduce pest damage through physical barriers (e.g., cuticle thickness), or

Table 1
Crop diversification strategies over spatial scales.

Crop diversification strategy	Definition	Spatial scale
Intercropping	Association of a secondary crop grown simultaneously with the main crop for most of their growth cycle. This includes undersown grass/clover, strip cropping (the two crops grown in alternate strips), push–pull (usually the push component is a secondary crop deterring pests from in-field towards the pull, an attractive plant grown at the border of the field)	field
Agroforestry	Inclusion of woody perennial crops (trees and shrubs, including timber, coppice, orchard trees, vines) in annual crop fields. This includes alley cropping (woody crops grown in alleys between strips of annual crops), silvoarable systems (woody crops in arable systems), silvopastures (woody crops in livestock systems)	field/farm
Cultivar mixtures	Mixture of cultivars (varieties, e.g. of cereal crops) grown and managed together in the field	field
Crop rotation	The succession of crops grown in a field and generally planned at farm-scale. In arable systems, this usually includes a rotation of cereal crops with legume crops. This also includes cover crops, usually sown in mixtures before spring crops to increase soil nutrients.	farm
Field size	The size of a field (delimited by its margins) can be adjusted at a farm to landscape scale.	farm/landscape
Landscape composition of crops	The diversity of crops found at a landscape scale (number of different crops and relative abundance in terms of soil occupancy)	landscape
Landscape configuration of crops	The spatial arrangement of crop diversity at a landscape scale: this includes field size, the distance between patches of the same crop, the shape of the patches, etc.	landscape

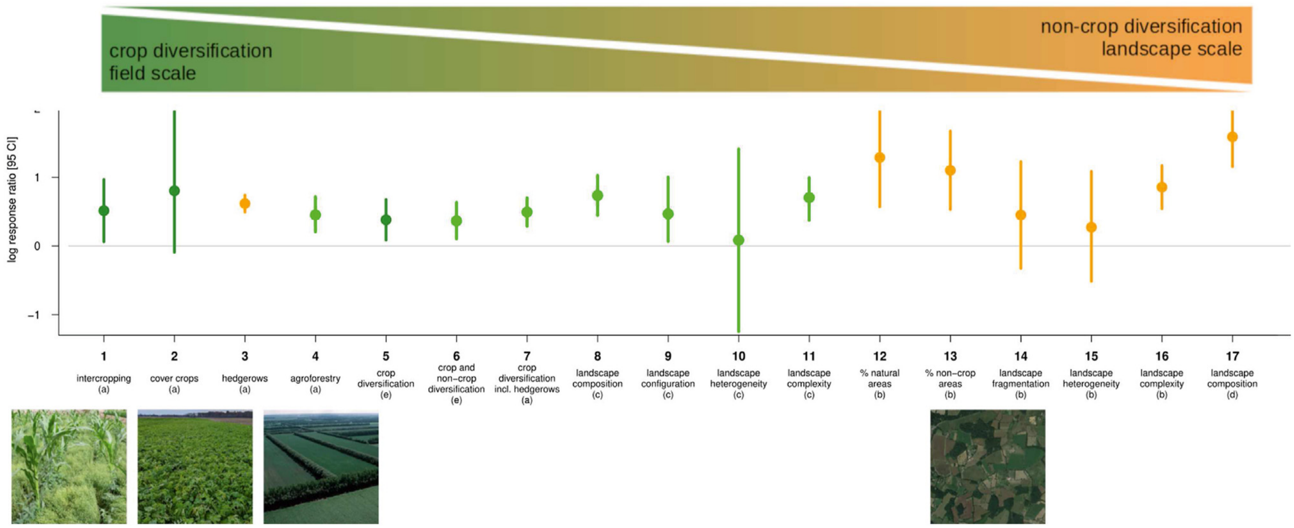

Fig. 1. Relative effect sizes (estimated median log of response ratio and 95% confidence interval) of crop and non-crop diversification measures on pest control metrics extracted from five meta-analyses: (a) (Beillouin et al., 2021 [85]); (b) (Tamburini et al., 2020 [21]); (c) (Estrada-Carmona et al., 2022 [39]); (d) (Duarte et al., 2018 [149]); and (e) (Karp et al., 2018 [150]). Effect sizes are ranked from field scale (left) to landscape scale (right). Dark green: crop diversification only measures; pale green: crop and non-crop diversification measures; orange: non-crop diversification measures only. See Table 2 for details on diversification measures and pest control metrics considered. Bold numbers 1–17 match that of Table 2, as well as in-text citation numbers.

chemical barriers (e.g., toxicity and repellent scent), while tolerance traits limit pest damage, e.g. through the reallocation of growth resources after tissue damage or through delayed phenology relative to arthropod pest life cycles [32]. Variety selection has traditionally relied on productivity, weakening crop defences, but both traditional breeding and modern genetics can be used to revert this trend [24,34]. Increasing the number of varieties with diverse resistance/tolerance traits at the field scale (cultivar mixtures) or at the landscape scale could therefore reduce pest pressure. This is also true at the species level, where functional diversification of crop species defence traits – both chemical and physical – could help reduce the densities of more generalist pests [34,35]. Diversifying resistance or tolerance traits in space and time can contribute to reducing levels of pest populations and avoid resistance breakdown (limiting selection pressure).

More generally, diversifying crops in space and time can break the resource spatio-temporal continuity for pests and thereby limit populations' build-up. The concentration of resources over large areas, i.e., spatial continuity, may favour arthropod pests (especially specialist species), and crop diversification reduces the probability for pests to find their host crop [36,37]. This largely relies on pest dispersal capacity, and therefore not only depends on landscape crop composition – the relative abundance of different crops in the landscape – but also on landscape crop configuration – the size, shape and spatial arrangement of crop patches [38,39]. However, diversifying crops in space and time can also favour, or at least have no effects, on generalist pest species [40]. Diversifying resources over time (reducing resource temporal continuity) can break pest life-cycle and therefore limit pest outbreaks [41]. The succession of crops in rotations must be chosen to maximise the crop functional diversity. This includes the diversity of resistance traits as presented above, and of particular interest for crops sensitive to virus transmitted by insect pests. However, crop rotations are often determined by other factors, including agronomic aspects (increase nutrient availability in the soil), the management of weed burden, and farming practices (soil cultivation, pesticide arsenal, …) [41,42].

2.2. *Top-down effects: promoting pest control delivered by natural enemies*

Top-down effects on arthropod herbivorous crop pests are mediated by the third trophic level, such as arthropod natural enemies [24]. Crop diversification may benefit natural enemies and the pest control service they deliver by providing the conditions to fulfil their nutritional and habitat requirements throughout their lifecycle, and by enhancing their movement at a local and landscape scale [13,43].

Most arthropod natural enemies of crop pests require a diversified diet incorporating prey/host resources and plant resources [12,13,45]. For omnivorous predators, plant resources encompass floral resources – pollen and nectar, and also plant tissues (e.g., mirid predators) [46] or seeds (e.g., omnivorous carabid beetles) [47], while they also prey on a diversity of species alternative to the main crop pest species. Pollen sources bring proteins [48] and nectar provides water and carbohydrates [49]. Alternative prey provide proteins, sugar and water. A mixed diet increases natural enemies' fitness (longevity, fecundity) and population growth [13,50,51]. Nectar as part of arthropods' diet increases the fitness of parasitoids, mirid bugs, lacewings, and ladybirds [44,52]. Crop diversification may enhance natural enemies by providing such diverse resources, either directly (e.g., flowering crops), or indirectly by hosting diverse communities of alternative herbivorous hosts/prey. Crop diversification may also increase the spatio-temporal continuity of all these key resources for natural enemies, enhancing their population growth and thereby promoting biological pest control. However, despite the known benefits of diverse diets and resource continuity, most studies investigate the effects of plant diversification (flowering plants and banker plant systems) where alternative plants are non-crop plants or at best non-productive crop plants [53–58]. There is a need to better identify how crop functional diversity itself may provide such diverse food resources without requiring the use of non-crop service plants [36,59].

Similarly to arthropod pests, arthropod natural enemies largely rely on chemical signals to locate their resources. They especially use herbivore-induced plant volatiles (HIPVs), which are emitted by crop plants upon attack by herbivores, to locate their main host/prey [60–62]. These chemical communication channels can be very specific, as is the case of the TPS10 (terpene synthase) produced by *Arabidopsis thaliana* attacked by *Spodoptera litura* and attracting the parasitoid wasp *Cotesia marginiventris* [61]. The high efficacy of HIPVs has been used to develop strategies such as push–pull (reviewed below) [13]. HIPVs can be used in direct diffusers in greenhouses [63,64], or through plant manipulation in fields [25]. Crop diversification manipulating the chemical diversity of crop plants, and especially their potential to emit HIPVs may thus promote biological pest control by attracting natural enemies into crop fields.

Table 2
Description of measures of crop and non-crop diversification included in meta-analyses and shown in Fig. 1.

[a]	Reference	Meta-analysis level	Number of meta-analyses included	Number of original comparisons	Measure	Spatial scale	Diversification strategy	Description of the measure considered in the meta-analysis	Description of the response variables
1	Beillouin et al. (2021) [85]	2nd order	8	1019	intercropping	field	crop	mixed intercropping, relay intercropping, strip intercropping, push–pull, inter-row grass cover	pest and disease control: damage quantification, disease prevalence, pest abundance, weed abundance, other (natural enemy abundance, …)
2			8	1948	cover crops	field, farm	crop	cover crops, grass strips	
3			2	13	hedgerows	local to landscape	non-crop	Hedgerows	
4			3	114	agroforestry	field	crop + non-crop	alley cropping, improved fallows (sequential agroforestry), hedgerows, multi-strata systems, parklands, shaded perennial crop-systems, silvoarable systems, silvopastures	
5	Tamburini et al. (2020) [21]	2nd order	14	1203	crop diversification	field	crop	cover cropping, intercropping, crop rotations, catch cropping, high field-level plant diversity, agroforestry	pest abundance and diversity, pest damage, potential natural enemy abundance, diversity and evenness, weed abundance and biomass
6			14	1203	crop and non-crop diversification	field to landscape	crop + non-crop	all of the above, plus landscape complexity, field margin diversity (e.g. grass margins, flower strips), field size, inter-row vegetation management, crop perenniality, parkland	
7	Beillouin et al. (2021) [85]	2nd order	12	3081	crop diversification incl. hedgerows	field to landscape	crop + non-crop	cover crops, intercropping, crop rotations, cultivar mixtures, agroforestry (including hedgerows, alley cropping, …)	pest and disease control: damage quantification, disease prevalence, pest abundance, weed abundance, other (natural enemy abundance, …)
8	Estrada-Carmona et al. (2022) [39]	1st order	NA	250	landscape composition	landscape	crop + non-crop	% non-crop areas, % annual crop, % cereal, % SNH (% fallow, % aquatic, % forest, %grassland)	natural enemies (total abundance, species richness, evenness)
9				44	landscape configuration	landscape	crop + non-crop	aggregation (field size, juxtaposition), proximity (distance from floral strips, from forest, from grassland, from SNH, landscape shape index, patch density), connectivity (% hedgerow, % riparian, % SNH linear, edge density, field boundary, crop edge, …)	
10				31	landscape heterogeneity	landscape	crop + non-crop	crop diversity, crop evenness, number of land use patches, flower abundance, flower richness, habitat diversity, land cover diversity	
11				337	landscape complexity	landscape	crop + non-crop	The three above: landscape composition, landscape configuration, landscape heterogeneity	natural enemies (total abundance, species richness, evenness)
12	Duarte et al. (2018) [149]	1st order	NA	23	% natural areas	landscape	non-crop	percent natural areas	natural enemies response (abundance, richness, diversity, direct effect on pest reduction)
13				33	% non-crop areas	landscape	non-crop	percent non-crop areas	
14				17	landscape fragmentation	landscape	non-crop	landscape fragmentation (number of patches, edge density, distance to SNH)	
15				17	landscape heterogeneity	landscape	non-crop	landscape heterogeneity (diversity, evenness and richness index of SNH)	
16				90	landscape complexity	landscape	non-crop	percent natural areas, percent non-crop areas, landscape aggregation, landscape heterogeneity, landscape connectivity, landscape fragmentation	
17	Karp et al. (2018) [150]	1st order	NA	359	landscape composition	landscape	non-crop	landscape composition in a 2 km radius (habitat categories: forest/trees, grassland, scrubland, annual cropland, perennial cropland, urban areas, other)	natural enemy total abundance, and activity (sentinels, cages)

[a] Bold numbers 1–17 correspond to the effect sizes 1–17 shown in Fig. 1. SNH: semi-natural habitat.

Beyond diversified food resources, the provision of habitats is essential to enhance the activity and abundance of natural enemies. Natural enemies require shelter/refuges from perturbations such as crop cultivation, harvest, pesticide applications, predation, and weather variations [13,65,66]. The presence of local overwintering sites is also important to ensure an early colonisation of crop fields in the Spring, preventing pest outbreaks [67,68]. Increasing within-field crop diversity can benefit the activity, abundance and diversity of natural enemies of pests by offering shelter or overwintering sites 90. For instance, parsley intercropped in cabbage can increase humidity, thereby enhancing natural enemy abundance [69]. Similarly, coriander intercropped in cabbage can reduce intraguild predation of ladybirds on lacewings, by providing shelter through the complex leaf structures [70]. Also, cover crops providing ground cover can accelerate field recolonisation from overwintering sites in semi-natural habitats [67,71]. Increasing the functional complementarity of crops in space and time at larger scales may also significantly increase the availability of refuges or overwintering sites that would in the end benefit top-down control of pests. For instance, mixing perennial and annual crops in the same landscape such as agroforestry systems, may increase the availability of shelter sites for natural enemies in agricultural landscapes [72,73].

Finally, enhancing natural enemies' movement at local and landscape scales is essential for biological control efficacy, since it increases the likelihood of pest patches detection by natural enemies. Landscape crop composition and configuration increasing habitat and food resources spatio-temporal continuity can enhance the movement of natural enemies and their colonisation of crop fields [39,74,75]. Differential crop phenology in diversified crop mosaics may enhance natural enemy spillover [40,76,77], i.e., the exportation of a population from one patch to another, following a strong population growth [78].

3. Implementing crop diversification through spatial scales

Diverse crop diversification measures enhancing natural enemies and biological pest control services are applicable over a range of spatial scales. The most relevant scale depends on the cropping system and on pest and natural enemy ecology [79]. For instance, predator density in wheat fields was found to respond positively to crop diversification within a 100–250 m radius, while parasitoid density responded positively to crop diversification within a 2–3 km radius [80]. Conversely, a meta-analysis found that generalist natural enemies were influenced by landscape complexity over various scales (from 500 m to 5 km), while specialists such as parasitoids responded most significantly to smaller scales only [16]. Finally, non-linear responses of natural enemies to crop diversification may also be expected [81].

3.1. Field scale

A field is a cropping unit, often cropped with a single crop type and usually separated from other fields by non-cropped field margins. Field-scale crop diversification practices have been known and used for decades. The most basic diversification of monoculture is the use of cultivar mixtures to create a locally genetically heterogeneous landscape by varying variety chemistry and resistance to pest attacks, thereby regulating pest populations [82]. Cultivar mixtures are especially relevant for crop disease management [83], but the chemical diversity (plant odours) could be more important for pest control than cultivar diversity, because it influences natural enemy foraging behaviour [84].

Intercropping is the simultaneous or relay cultivation of multiple crops over a growing season in the same field [85]. This includes companion cropping, strip cropping and relay intercropping. Most often, a legume crop is intercropped in cereal fields, e.g. maize-peanut, but vegetables can also be associated, and sometimes two cereal crops are associated, such as wheat and maize [86–88]. With different characteristics and phenology than the main crop, intercrops extend the range of food resources available to natural enemies, including flowering resources or alternative prey [89], and shelter from adverse weather [88]. Intercrops, emitting their own VOCs, can also dilute and mix the chemical signal of the main crop, confusing the detection of the main host crop plant by insect pests [88]. Finally, intercrops could potentially increase crop health and resistance to pest attacks by making soil nutrients more available [91,92]. Intercrops can therefore be also qualified as service crops or companion crops, due to their multifunctional role in pest control and beyond [93,94].

The success of intercropping relies on a deep understanding of the synergistic mechanisms between the associated crops, and its effects on biological pest control have been assessed as overall positive although quite variable in a meta-analysis (Fig. 1: 1) [85]. For instance, intercropping maize in wheat fields was found to enhance natural enemy populations of both parasitoids and predators, and thereby the control of wheat aphids [86]. Similarly, in organic farming systems, mixed cropping was found to significantly increase the intensity of biological pest control, with pest population densities three times lower than in cereal-only systems [95]. Finally, strip intercropping of wheat and oilseed rape led to a significant decline in aphid abundance and pollen beetles, increased aphid parasitism rate, and increased evenness of the predator community [96]. However, intercropping of legume crops in cereal fields did not increase aphid parasitism rate [97]. Generalist parasitoids were more represented in mixed cropping systems, and so were hyperparasitoids, leading to an increased hyperparasitism rate, a possible reason for the limited effect of intercropping on aphid control in this system [97].

Intercropping may involve disruptive and/or trap crops. One special case is push–pull systems. These are two-component systems relying mostly on semiochemicals to deter pests from the main crop (push) and attract them to a trapping system or a trap plant placed at the field margin (pull) [24]. The push component is often a repellent intercrop, while trap plants must be attractive and reduce the fitness of pests compared to the main crop [98]. The most famous push–pull system is intercropping *Desmodium intortum* in maize fields and planting *Brachiara* as a border trap crop [99]. This resulted in a 83% reduction in the number of larvae of the pest *Spodoptera frugiperda* per maize plant, and a 87% reduction in crop damage [99].

Agroforestry – the inclusion of perennial woody vegetation such as trees and shrubs in cropping systems – is considered a type of crop diversification in some studies, since such perennial trees can provide goods [85]. Agroforestry has an overall positive effect on biological pest control as shown in two meta-analyses (Fig. 1: 4) [21,85]. Beyond alley cropping with production trees, agroforestry also encompasses silvoarable systems and sylvopastures, shaded perennial crop systems, and even hedgerows, which are more often classified as a non-crop diversification practice (Fig. 1: 3,4) [85]. Such woody, perennial structures provide shelter for natural enemies, and refuges from perturbations such as extreme weather, pesticide applications, soil cultivation and harvest [72,100].

3.2. Farm scale

A farm is a commercial exploitation, usually managing a piece of land composed of several fields but managed under the same farming plan. The farm scale corresponds to this land unit, and may incorporate semi-natural habitat in addition to the different fields. However, we only consider crop diversification in these multiple fields managed together here. Crop diversity – including the use of cover crops – at the farm scale can promote pest control, as shown by two meta-analyses (Fig. 1: 2,5) [21,85]. This includes all elements of crop rotation (rotation length and diversity, cover cropping, catch cropping) as well as structural perennial elements, e.g. woody crops in agroforestry schemes, which contribute to diversifying the potential sources of alternative resources and shelter habitats for natural enemies [21,73,85]. Due to their perenniality, such crops need to be managed at a farm scale, although they are usually considered a field-scale crop diversification practice. Crop rotations are the most important driver of farm-scale crop diversity. Diverse crop rotations contribute to pest control by interrupting pest life cycles, and can also temporarily deprive pests of habitat and resources, thus delaying potential pest population build-up [102,103]. Crop rotations combining diverse annual crops with fallows or leys are especially important to reduce weed burden, notably by increasing competition and species richness of the weed community [42,104].

One aspect of crop rotations is the use of cover crops, which are usually grown before spring cash crops to increase soil nutrient availability to the main crop [105]. Cover crops may also promote biological pest control as shown in a meta-analysis (Fig. 1: 2) [85], notably by providing shelter to natural enemies [67]. Cover crop diversity is manipulated at the field scale to best match the specific needs of the local farming system. Cover crop diversity was found to enhance the abundance of natural enemies, strengthening the associated biological pest control service, especially in landscapes with low semi-natural habitat proportion [106].

The temporal dimension in crop rotations and crop diversity at farm scale more generally can promote natural enemy movement. For instance, crop succession or differential crop phenology can induce natural enemy spillover from a source crop to a sink crop: the source may be a harvested field, or a senescent crop providing reduced resources and shelter to natural enemies, while the sink will be a more attractive crop, often at an earlier growing stage and hosting prey [40,75,77,107,108].

3.3. Landscape scale

An agricultural landscape is a large, relatively heterogeneous area, composed of multiple farms and of semi-natural habitats, where farms share similarities (e.g., in the types of crops and outlets produced, in the abiotic environment, etc.). The landscape-scale management of crop diversity is essential, since benefits of crop diversification at smaller scales (farm or field) are not necessarily propagated to the landscape scale [14,109]. Both landscape composition – the diversity and relative abundance of different habitats or soil use types, including landscape-scale crop diversity – and landscape configuration – the spatial arrangement of these different patches or fields, which is their distribution, density and shapes, fragmentation and connectivity (e.g., distance between similar patches) – are important to promote pest control, since they affect the continuous availability of alternative food resources and habitats, but also the movement capacity of invertebrate pests and natural enemies [38,39,44,110,111]. Crop diversification at a landscape to regional scales can help conserve arthropod biodiversity (beta-diversity, the regional pool of natural enemy diversity) and thereby biological pest control services that are resilient to perturbations such as the emergence of new invasive pests [112–114].

Crop diversification at the landscape scale should seek to increase the number of crops and maximise their functional diversity to promote biological pest control, e.g. by diversifying their phenology (annual, pluri-annual, perennial) and family (cereal, legume …; Fig. 1: 1–8) [39,101]. One function to consider is the heterogeneity in crop nutrients and defences, which could reduce herbivore fitness [115,116]. Besides composition, crop diversification at the landscape scale can increase landscape heterogeneity by manipulating the configuration of crop patches (the crop mosaic) and by reducing field size, both promoting biological pest control without reducing cropland productivity [17,103,113,117,118].

The amount of semi-natural habitats in the landscape is known to shape the natural enemy's species pool in agricultural landscapes [9,17]. Such semi-natural habitats (e.g., grasslands, forests or hedgerows), which are a non-crop diversification measure, are comparatively less disturbed than crop fields, and they offer a large diversity of resources for natural enemies. Natural enemies usually colonize crop fields from semi-natural habitats at the end of the overwintering season, and the spillover of natural enemies at the crop/non-crop interface therefore shapes the top-down control of pests in crop fields [119,120]. Because crop diversification in space and time can increase the spatio-temporal continuity of resources and availability of habitats for natural enemy communities, a synergistic effect between the quantity of semi-natural habitats and crop diversity on top-down control of pests may be expected, where semi-natural habitats allow the maintenance of a natural enemy species pool and crop diversification enhances their maintenance in fields. However, this synergistic effect is only valid if crop diversification is designed to benefit natural enemies (the natural enemies hypothesis) and limit pest populations (the resource concentration hypothesis). We also expect a non-linear relationship between the amount of semi-natural habitats and crop diversity on pest control. Following the intermediate landscape complexity hypothesis [121], no strong effect of crop diversification would be expected in extremely simplified landscapes with no semi-natural habitats and hence extremely limited sources of natural enemies, or in highly complex landscapes already providing important resources and habitats for natural enemies (mass effects). A maximum effect size of crop diversification is expected at intermediate levels of landscape complexity, where natural enemy communities colonizing crop fields from semi-natural habitats can benefit from the increased spatio-temporal continuity of resources mediated by crop diversification. Although no strong empirical test of this hypothesis exists, several studies reported an interactive effect between semi-natural habitats (SNH) and crop diversification that tend to valid this hypothesis. Crop diversity was found to benefit carabid beetles in landscapes with SNH only, compared to landscapes with no SNH [122]. Similarly, a meta-analysis showed that in-field plant diversity increased arthropod abundance and species richness (especially of rare species) in complex landscapes only (>20% SNH areas) [123]. Conversely, cover cropping had a higher positive effect on natural enemy abundance and predation rate in more simple landscapes (<50% SNH) compared to more complex landscapes (>50% SNH) [106].

At a landscape scale too, temporal dynamics play a role in shaping pests and natural enemy population dynamics due to their migration capacity. For instance, in a cropland mosaic including oilseed rape grown over variable areas across the landscape from year to year, the abundance of pest pollen beetles in oilseed rape was higher in years when the oilseed rape-grown area was strongly reduced relative to the previous year [124]. Similarly, carabid beetle species richness (especially of granivorous beetles) was found to be higher in landscapes with higher crop diversity in the previous year [125].

4. Multi-service provisioning of crop diversification

In addition to arthropod pest control, crop diversification provides other benefits for agroecosystem functioning. It is also beneficial to weed or disease control, and promotes soil fertility, carbon sequestration, nutrient cycling, water regulation and quality, and agricultural productivity (reviewed in two second-order meta-analyses [21,85]. Because these other benefits may influence farmers' choices in adopting crop diversification strategies, we briefly cover the other benefits here to highlight the need for integrating pest management with other aspects of farming systems.

Crop diversification enhances soil health through the diversity of the microbial community and of crop functions, root systems and nutrient use, favouring nutrient cycling and soil fertility, low compaction, reduced erosion and carbon sequestration, with positive consequences on water quality and regulation [88,126]. By preserving soil and sequestering carbon, crop diversification also reduces greenhouse gases emissions, mitigating climate change [85,127], although the number of studies directly measuring the effects of crop diversification on climate regulation remains very low [21].

Beyond climate regulation, and of interest to farmers, crop diversification can increase the resilience of farming systems to climate change and extreme events [128]. This notably happens through the processes above, including preserving and restoring soil health and higher nutrient and water use efficiency [88]. Diversifying crop rotations increases agrosystem-level stress resistance, and therefore the resilience of agricultural productivity to climate change [129]. From an economic point of view, farmers facing an increasing unpredictability of extreme climatic events may rely on crop diversification to secure a stable agricultural production [130,131]. Although crop diversification practices may be implemented by farmers for other goals than pest regulation primarily, it could be useful and more efficient to consider how crop diversification may synergistically enhance several ecosystem services in an integrated approach [132].

5. Agronomic and socio-economic limits to crop diversification

Despite the multiple benefits of crop diversification, not all crop diversification practices are easy to implement or widely accepted by farmers. Crop diversification strategies at field- or farm-scale are intrinsically related to farm management and planning. Diversifying crop rotations is by far the preferred crop diversification strategy by EU farmers, while in-field crop diversification practices such as mixed cropping, cover crops, and undersowing spring cereals were the least preferred, even less so than semi-natural habitat management (woodland, hedgerows, grass margins) [19]. This may be because crop rotations have a long history in traditional farming, while mixed cropping practices are knowledge-intensive [88].

Knowledge access affects farmers' perception of the importance of ecological regulations and ecosystem services for agricultural productivity [133]. This knowledge barrier is also caused by the long history of pesticide applications as a close to systematic response to pest problems, resulting in a socio-technical lock-in where adopting new integrated pest management practices is perceived as risky (fear of reducing yields and profit and uncertainty of new techniques) [134,135]. One way to overcome knowledge limitation is to empower farmers in co-production processes where farmers and scientists work together to demonstrate and achieve higher uptake [136]. The importance of peer-to-peer learning through farmers' networks is also essential for the uptake of novel or complex practices [136,137].

The perceived uncertainty on the profitability of crop diversification techniques is not necessarily supported by the literature. While crop diversification may increase labour effort [88], a meta-analysis of 3192 effect sizes from 119 articles showed that diversified farming systems are at least as profitable as simplified farming systems [138]. In average, total costs and profits were higher than in simplified systems, but the benefit-cost ratio was equivalent [138].

Beyond knowledge and perceived economic risks, field-level crop diversification techniques are technically, economically and biologically constrained. Technical limitations come from available machinery, which constrains field size and possible crop associations. For instance, mixed cropping may require specific drilling and harvesting/grain sorting machinery [139]. Economically, mixed cropping at the species- or variety-levels (e.g. mixed wheat cultivar) may impact harvested grain quality established by industrial standards, with an impact on commodity price, but also local specific outlets [140,141]. This may also require growing less profitable crops to increase cultivated crop diversity. Biological limitations of crop diversification at the field- and farm-scales are diverse. Pedoclimatic variability at the farm scale may prevent full rotations over the entire farmland where soil conditions prevent optimal growth of some crops [142,143]. Crop associations at the field scale are constrained by the requirements of each crop for nutrients, light and water to minimize competition and avoid allelopathic effects, and only synergistic crop associations can be used [91,144–146].

The landscape scale is essential for effective diversification strategies promoting ecosystem services, but this is also the most complex from a socio-economic point of view [109]. This is because of the diversity of actors and structures from the farming, industry and political communities, who usually do not strongly interact. Therefore, landscape crop diversification requires efficient communication and a strong multi-actor coordination of diversification strategies to efficiently promote biological pest control and other ecosystem services [109,134]. This can only be achieved through political and financial incentives, and strong farmers' networks [19,137,147], but industrial lock-ins also need to be lifted up. For instance, cropping systems are often organised at a regional scale through agri-food value chains, limiting commodity outlets of locally rarer crops [137,148].

6. Conclusion and perspectives

We reviewed the main crop diversification strategies available at the field (including intercropping, cultivar mixtures), farm (crop rotations), and landscape scales (field size, landscape composition, landscape configuration; Table 1). Field- and farm-scale crop diversification measures may be easier to implement, because they depend on farmland decisions, whereas landscape-scale measures require a coordination between a diversity of actors over large geographic areas. In both cases however, crop diversification is only possible if specific outlets for newly introduced crops are available locally. We compiled summary effect sizes from meta-analyses of diversification measures on biological pest control, and we show that the potential of crop diversification for promoting biological pest control is as high as that of non-crop diversification measures (Fig. 1). However, despite the advances in modern statistics and common metrics allowing a comparison of effect sizes from extremely diverse original studies, these comparisons must be undertaken with caution, due to the different sets of explanatory variables and responses variables related to biological pest control used across meta-analyses (Table 2). This also highlights the difficulty to reliably estimate the relative importance and interactive effects of diversification measures, notably due to an uneven number of studies at a global scale, the heterogeneity in quantified response variables, and the complexity of multi-factorial studies (e.g., experimenting the relative effects of multiple drivers across scales). Future research should aim to quantify the synergistic effects of diverse diversification measures, especially of crop and non-crop diversification, on unambiguous measures of biological pest control (including predation and parasitism rate, pest damage and crop productivity) across spatial scales and in a diversity of ecological contexts. The field also clearly lacks specific recommendations applicable in a variety of cropping systems such as the number and functional characteristics of crops to be associated and their spatial arrangement across spatio-temporal scales.

Because crop diversification strategies are implemented by farmers and do not reduce cultivated land areas or agricultural productivity, they could be prioritized by farmers over non-crop diversification measures [20,21]. However, crop and non-crop diversification measures often function synergistically, and both are essential at a landscape scale to maintain a diverse community of natural enemies and resilient biological pest control services. Finally, crop diversification has many more benefits than biological pest control, including for soil health, climate mitigation and stable agricultural productivity. It is therefore relevant to integrate those multiple dimensions of crop diversification beyond pest control, in a systematic approach to agriculture. Empowering farmers with easy access to knowledge and practical solutions, large-scale coordination and profitable economic avenues is key for a wider uptake of crop diversification practices. This will require transformative co-production efforts gathering farmers, scientists and policymakers.

Declaration of interests

N.D. is a Managing Editor of Agriculture Communications, but was not involved in the peer-review process of this article. The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: N.D. reports financial support was provided by European Union.

Acknowledgments

This work was supported by the EUCLID project funded by the European Union programme H2020 (Grant Number 633999), and by the ADOPT-IPM project funded by the European Union programme Horizon Europe (grant Number 101060430).

Authors' contributions

C.C.J., **E.T.** and **A.R.** wrote the manuscript; **A.V.L.**, **N.D.** and **S.W.** contributed ideas and proofread the manuscript; **N.D.** secured funding. All authors agreed to co-author the manuscript.

References

[1] Pingali PL. Green Revolution: impacts, limits, and the path ahead. Proc Natl Acad Sci USA 2012;109:12302–8.
[2] FAO. Human energy requirements. Report of a Joint FAO/WHO/UNU Expert Consultation, FAO Food and nutrition technical report series 1. Rome. 2001.
[3] Oerke EC. Crop losses to pests. J Agric Sci 2006;144:31–43.
[4] Desneux N, Decourtye A, Delpuech JM. The sublethal effects of pesticides on beneficial arthropods. Annu Rev Entomol 2007;52:81–106.
[5] Zhang L, Rana I, Shaffer RM, Taioli E, Sheppard L. Exposure to glyphosate-based herbicides and risk for non-Hodgkin lymphoma: a meta-analysis and supporting evidence. Rev Mutat Res 2019;781:186–206.
[6] Raven PH, Wagner DL. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proc Natl Acad Sci USA 2021;118:e2002548117.
[7] Eilenberg J, Hajek A, Lomer C. Suggestions for unifying the terminology in biological control. BioControl 2001;46:387–400.
[8] Tittonell P. Ecological intensification of agriculture – sustainable by nature. Curr Opin Environ Sustain 2014;8:53–61.
[9] Tscharntke T, Bommarco R, Clough Y, Crist TO, Kleijn D, Rand TA, et al. Conservation biological control and enemy diversity on a landscape scale. Biol Control 2008;45:238–53.
[10] Malaj E, Morrissey CA. Increased reliance on insecticide applications in Canada linked to simplified agricultural landscapes. Ecol Appl 2022;32:e2533.
[11] Greenop A, Cook SM, Wilby A, Pywell RF, Woodcock BA. Invertebrate community structure predicts natural pest control resilience to insecticide exposure. J Appl Ecol 2020;57:2441–53.
[12] Lundgren JG. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. Biol Control 2009;51:294–305.
[13] Gurr GM, Wratten SD, Landis DA, You M. Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol 2017;62:91–109.
[14] Schneider MK, Lüscher G, Jeanneret P, Arndorfer M, Ammari Y, Bailey D, et al. Gains to species diversity in organically farmed fields are not propagated at the farm level. Nat Commun 2014;5:4151.
[15] He X, Weisser W, Zou Y, Fan S, Crowther TW, Wanger TC. Integrating agricultural diversification in China's major policies. Trends Ecol Evol 2022;37:819–22.
[16] Chaplin-Kramer R, O'Rourke ME, Blitzer EJ, Kremen C. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol Lett 2011;14:922–32.
[17] Rusch A, Chaplin-Kramer R, Gardiner MM, Hawro V, Holland J, Landis D, et al. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. Agric Ecosyst Environ 2016;221:198–204.
[18] Tscharntke T, Karp DS, Chaplin-Kramer R, Batáry P, DeClerck F, et al. When natural habitat fails to enhance biological pest control – five hypotheses. Biol Conserv 2016;204:449–58.
[19] Kleijn D, Bommarco R, Fijen TPM, Garibaldi LA, Potts SG, van der Putten WH. Ecological intensification: bridging the gap between science and practice. Trends Ecol Evol 2019;34:154–66.
[20] Sirami C, Gross N, Baillod AB, Bertrand C, Carrié R, Hass A, et al. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc Natl Acad Sci USA 2019;116:16442–7.
[21] Tamburini G, Bommarco R, Wanger TC, Kremen C, van der Heijden MGA, Liebman M, et al. Agricultural diversification promotes multiple ecosystem services without compromising yield. Sci Adv 2020;6:eaba1715.
[22] Desneux N, Han P, Mansour R, Arnó J, Brévault T, Campos MR, et al. Integrated pest management of *Tuta absoluta*: practical implementations across different world regions. J Pest Sci 2021;95:17–36.
[23] Liang Y, Chen X, Dai H, Wang J, Guo X, Wang S, et al. Flower provision reduces intraguild predation between predators and increases aphid biocontrol in tomato. J Pest Sci 2022;95:461–72.
[24] Han P, Lavoir AV, Rodriguez-Saona C, Desneux N. Bottom-up forces in agroecosystems and their potential impact on arthropod pest management. Annu Rev Entomol 2022;67:239–59.
[25] Cook SM, Khan ZR, Pickett JA. The use of push-pull strategies in integrated pest management. Annu Rev Entomol 2007;52:375–400.
[26] van der Kooi CJ, Stavenga DG, Arikawa K, Belušič G, Kelber A. Evolution of insect color vision: from spectral sensitivity to visual ecology. Annu Rev Entomol 2021;66:435–61.
[27] Döring TF, Kirchner SM. A model for colour preference behaviour of spring migrant aphids. Phi Trans Roy Soc B 2022;377:20210283.
[28] Zhang Z, Zhang B, He H, Yan M, Li J, Yan F. Changes in visual and olfactory cues in virus-infected host plants alter the behavior of *Bemisia tabaci*. Front Ecol Evol 2022;10.
[29] Lund M, Brainard DC, Szendrei Z. Cue hierarchy for host plant selection in *Pieris rapae*. Entomol Exp Appl 2019;167:330–40.
[30] Szendrei Z, Rodriguez-Saona C. A meta-analysis of insect pest behavioral manipulation with plant volatiles. Entomol Exp Appl 2010;134:201–10.
[31] Bouwmeester H, Schuurink RC, Bleeker PM, Schiestl F. The role of volatiles in plant communication. Plant J 2019;100:892–907.
[32] Cook SM, Smart LE, Martin JL, Murray DA, Watts NP, Williams IH. Exploitation of host plant preferences in pest management strategies for oilseed rape (*Brassica napus*). Entomol Exp Appl 2006;119:221–9.
[33] Tooker JF, Frank SD. Genotypically diverse cultivar mixtures for insect pest management and increased crop yields. J Appl Ecol 2012;49:974–85.
[34] Mitchell C, Brennan RM, Graham J, Karley AJ. Plant defense against herbivorous pests: exploiting resistance and tolerance traits for sustainable crop protection. Front Plant Sci 2016;7.
[35] Hasanuzzaman ATM, Islam MN, Liu FH, Cao HH, Liu TX. Leaf chemical compositions of different eggplant varieties affect performance of *Bemisia tabaci* (Hemiptera: Aleyrodidae) nymphs and adults. J Econ Entomol 2017;111:445–53.
[36] González-Chang M, Tiwari S, Sharma S, Wratten SD. Habitat management for pest management: limitations and prospects. Ann Entomol Soc Am 2019;112:302–17.
[37] Kheirodin A, Cárcamo HA, Costamagna AC. Contrasting effects of host crops and crop diversity on the abundance and parasitism of a specialist herbivore in agricultural landscapes. Landsc Ecol 2020;35:1073–87.
[38] Martin EA, Dainese M, Clough Y, Báldi A, Bommarco R, Gagic V, et al. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol Lett 2019;22:1083–94.
[39] Estrada-Carmona N, Sánchez AC, Remans R, Jones SK. Complex agricultural landscapes host more biodiversity than simple ones: a global meta-analysis. Proc Natl Acad Sci USA 2022;119:e2203385119.
[40] Jaworski CC, Thomine E, Rusch A, Lavoir AV, Xiu C, Ning D, et al. At which spatial scale does crop diversity enhance natural enemy populations and pest control? An experiment in a mosaic cropping system. Agronomy 2022;12:1973.
[41] Shah KK, Modi B, Pandey HP, Subedi A, Aryal G, Pandey M, et al. Diversified crop rotation: an approach for sustainable agriculture production. Adv Agric 2021;2021:1–9.
[42] Weisberger D, Nichols V, Liebman M. Does diversifying crop rotations suppress weeds? A meta-analysis. PLoS One 2019;14:1–12.
[43] Zhao J, Yang Y, Zhang K, Jeong J, Zeng Z, Zang H. Does crop rotation yield more in China? A meta-analysis. Field Crop Res 2020;245:107659.
[44] Schellhorn NA, Gagic V, Bommarco R. Time will tell: resource continuity bolsters ecosystem services. Trends Ecol Evol 2015;30:524–30.
[45] Wäckers FL, van Rijn PCJ. Pick and mix: selecting flowering plants to meet the requirements of target biological control insects. In: Gurr GM, Wratten SD, Snyder WE, Read DMY, editors. Biodiversity and insect pests. John Wiley & Sons, Ltd; 2012. p. 139–65.
[46] Li W, Wang L, Jaworski CC, Yang F, Liu B, Jiang Y, et al. The outbreaks of nontarget mirid bugs promote arthropod pest suppression in Bt cotton agroecosystems. Plant Biotechnol J 2020;18:322–4.
[47] Kulkarni SS, Dosdall LM, Willenborg CJ. The role of ground beetles (Coleoptera: Carabidae) in weed seed consumption: a review. Weed Sci 2015;63:355–76.
[48] Vaudo AD, Patch HM, Mortensen DA, Tooker JF, Grozinger CM. Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences. Proc Natl Acad Sci USA 2016;113:E4035–42.
[49] Heil M. Nectar: generation, regulation and ecological functions. Trends Plant Sci 2011;16:191–200.
[50] Jaworski CC, Chailleux A, Bearez P, Desneux N. Apparent competition between major pests reduces pest population densities on tomato crop, but not yield loss. J Pest Sci 2015;88:793–803.
[51] Wang Y, Yao F, Soares MA, Basiri SE, Amiens-Desneux E, Campos MR, et al. Effects of four non-crop plants on life history traits of the lady beetle *Harmonia axyridis*. Entomol Gen 2020;40:243–52.
[52] Gillespie MAK, Gurr GM, Wratten SD. Beyond nectar provision: the other resource requirements of parasitoid biological control agents. Entomol Exp Appl 2016;159:207–21.
[53] Tylianakis JM, Didham RK, Wratten SD. Improved fitness of aphid parasitoids receiving resource subsidies. Ecology 2004;85:658–66.
[54] Arnó J, Oveja MF, Gabarra R. Selection of flowering plants to enhance the biological control of *Tuta absoluta* using parasitoids. Biol Control 2018;122:41–50.
[55] Haan NL, Iuliano BG, Gratton C, Landis DA. Chapter Five - designing agricultural landscapes for arthropod-based ecosystem services in North America. In: Bohan DA, Vanbergen AJ, editors. The Future of agricultural landscapes, Part II, advances in ecological research. Academic Press; 2021. p. 191–250.
[56] Li S, Jaworski CC, Hatt S, Zhang F, Desneux N, Wang S. Flower strips adjacent to greenhouses help reduce pest populations and insecticide applications inside organic commercial greenhouses. J Pest Sci 2021;94:679–89.
[57] Chen X, Jaworski CC, Dai H, Liang Y, Guo X, Wang S, et al. Combining banker plants to achieve long-term pest control in multi-pest and multi-natural enemy cropping systems. J Pest Sci 2022;95:685–97.
[58] Yang Q, Liu Z, Ouyang F, Men X, Zhang K, Liu M, et al. Flower strips promote natural enemies, provide efficient aphid biocontrol, and reduce insecticide requirement in cotton crops. Entomol Gen 2022.
[59] Colazza S, Peri E, Cusumano A. Chemical ecology of floral resources in conservation biological control. Annu Rev Entomol 2023;68:13–29.

[60] Heil M, Karban R. Explaining evolution of plant communication by airborne signals. Trends Ecol Evol 2010;25:137–44.
[61] War AR, Sharma HC, Paulraj MG, War MY, Ignacimuthu S. Herbivore induced plant volatiles: their role in plant defense for pest management. Plant Signal Behav 2011;6:1973–8.
[62] Pérez-Hedo M, Alonso-Valiente M, Vacas S, Gallego C, Rambla JL, Navarro-Llopis V, et al. Eliciting tomato plant defenses by exposure to herbivore induced plant volatiles. Entomol Gen 2021;41:209–18.
[63] Kaplan I. Attracting carnivorous arthropods with plant volatiles: the future of biocontrol or playing with fire? Biol Control 2012;60:77–89.
[64] Ingwell LL, Avila-Ruiz DA, Foster R, Kaplan I. Tailoring insect biocontrol for high tunnels. Biol Control 2018;123:76–86.
[65] Landis DA, Wratten SD, Gurr GM. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu Rev Entomol 2000;45:175–201.
[66] Griffiths GJK, Holland JM, Bailey A, Thomas MB. Efficacy and economics of shelter habitats for conservation biological control. Biol Control 2008;45:200–9.
[67] Lundgren JG, Fergen JK. The effects of a winter cover crop on *Diabrotica virgifera* (Coleoptera: Chrysomelidae) populations and beneficial arthropod communities in no-till maize. Environ Entomol 2010;39:1816–28.
[68] Jaworski CC, Xiao D, Xu Q, Ramirez-Romero R, Guo X, Wang S, et al. Varying the spatial arrangement of synthetic herbivore-induced plant volatiles and companion plants to improve conservation biological control. J Appl Ecol 2019;56:1176–88.
[69] Gontijo LM, Saldanha AV, Souza DR, Viana RS, Bordin BC, Antonio AC. Intercropping hampers the nocturnal biological control of aphids. Ann Appl Biol 2018;172:148–59.
[70] da Silva AC, Cahú RC, Cogitskei MM, Kubota KSG, Sujii ER, Togni PHB. Intercropping collard plants with coriander modulates behavioral interactions among aphidophagous predators by altering microhabitat structure. Biol Control 2022;176:105084.
[71] Karamaouna F, Kati V, Volakakis N, Varikou K, Garantonakis N, Economou L, et al. Ground cover management with mixtures of flowering plants to enhance insect pollinators and natural enemies of pests in olive groves. Agric Ecosyst Environ 2019;274:76–89.
[72] Gontijo LM. Engineering natural enemy shelters to enhance conservation biological control in field crops. Biol Control 2019;130:155–63.
[73] Pan H, Liu B, Jaworski CC, Yang L, Liu Y, Desneux N, et al. Effects of aphid density and plant taxa on predatory ladybeetle abundance at field and landscape scales. Insects 2020;11:695.
[74] Schellhorn NA, Bianchi FJJA, Hsu CL. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. Annu Rev Entomol 2014;59: 559–81.
[75] Aviron S, Poggi S, Varennes YD, Lefèvre A. Local landscape heterogeneity affects crop colonization by natural enemies of pests in protected horticultural cropping systems. Agric Ecosyst Environ 2016;227:1–10.
[76] Jiao Z, Jaworski CC, Lu Y, Ye L, Wu K, Desneux N. Maize fields are a potential sink for an outbreaking mirid bug pest in Chinese Bt-cotton agricultural landscapes. Agric Ecosyst Environ 2019;279:122–9.
[77] Thomine E, Rusch A, Supplisson C, Monticelli LS, Amiens-Desneux E, Lavoir AV, et al. Highly diversified crop systems can promote the dispersal and foraging activity of the generalist predator *Harmonia axyridis*. Entomol Gen 2020;40: 133–45.
[78] Blitzer EJ, Dormann CF, Holzschuh A, Klein AM, Rand TA, Tscharntke T. Spillover of functionally important organisms between managed and natural habitats. Agric Ecosyst Environ 2012;146:34–43.
[79] Haan NL, Zhang Y, Landis DA. Predicting landscape configuration effects on agricultural pest suppression. Trends Ecol Evol 2020;35:175–86.
[80] Redlich S, Martin EA, Steffan-Dewenter I. Landscape-level crop diversity benefits biological pest control. J Appl Ecol 2018;55:2419–28.
[81] Muneret L, Ricci B, Vialatte A, Aviron S, Ducourtieux C, Biju-Duval L, et al. Carabid beetles have hump-shaped responses to disturbance and resource gradients within agricultural landscapes. J Appl Ecol 2023;60:581–91.
[82] Duan X, Pan S, Fan M, Chu B, Ma Z, Gao F, et al. Cultivar mixture enhances crop yield by decreasing aphids. Agronomy 2022;12:335.
[83] Reiss ER, Drinkwater LE. Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield. Ecol Appl 2018;28:62–77.
[84] Hauri KC, Glassmire AE, Wetzel WC. Chemical diversity rather than cultivar diversity predicts natural enemy control of herbivore pests. Ecol Appl 2021;31: e02289.
[85] Beillouin D, Ben-Ari T, Malézieux E, Seufert V, Makowski D. Positive but variable effects of crop diversification on biodiversity and ecosystem services. Global Change Biol 2021;27:4697–710.
[86] Liu J, Yan Y, Ali A, Wang N, Zhao Z, Yu M. Effects of wheat-maize intercropping on population dynamics of wheat aphids and their natural enemies. Sustainability 2017;9.
[87] Yin W, Chai Q, Zhao C, Yu A, Fan Z, Hu F, et al. Water utilization in intercropping: a review. Agric Water Manag 2020;241:106335.
[88] Huss CP, Holmes KD, Blubaugh CK. Benefits and risks of intercropping for crop resilience and pest management. J Econ Entomol 2022;115:1350–62.
[89] Parker JE, Snyder WE, Hamilton GC, Rodriguez-Saona CR. Companion planting and insect pest control. In: Weed and pest control-conventional and new challenges. London, SW7 2QJ, UK: InTechOpen Limited; 2013, 55040.
[90] Pan H, Xiu C, Liu B, Wyckhuys KAG, Lu Y. Whorl-stage maize provides a microclimate refuge for predatory ladybeetles. Biol Control 2020;42:104162.
[91] Maitra S, Hossain A, Brestic M, Skalicky M, Ondrisik P, Gitari H, et al. Intercropping – a low input agricultural strategy for food and environmental security. Agronomy 2021;11:343.
[92] Li XF, Wang ZG, Bao XG, Sun JH, Yang SC, Wang P, et al. Long-term increased grain yield and soil fertility from intercropping. Nat Sustain 2021;4:943–50.
[93] Parolin P, Bresch C, Desneux N, Brun R, Bout A, Boll R, et al. Secondary plants used in biological control: a review. International. J Pest Manag 2012;58:91–100.
[94] Blassioli-Moraes MC, Venzon M, Silveira LCP, Gontijo LM, Togni PHB, Sujii ER, et al. Companion and smart plants: scientific background to promote conservation biological control. Neotrop Entomol 2022;51:171–87.
[95] Couthouis E, Aviron S, Pétillon J, Alignier A. Ecological performance underlying ecosystem multifunctionality is promoted by organic farming and hedgerows at the local scale but not at the landscape scale. J Appl Ecol 2023;60:17–28.
[96] Alarcón-Segura V, Grass I, Breustedt G, Rohlfs M, Tscharntke T. Strip intercropping of wheat and oilseed rape enhances biodiversity and biological pest control in a conventionally managed farm scenario. J Appl Ecol 2022;59:1513–23.
[97] Jeavons E, van Baaren J, Le Ralec A, Buchard C, Duval F, Llopis S, et al. Third and fourth trophic level composition shift in an aphid-parasitoid-hyperparasitoid food web limits aphid control in an intercropping system. J Appl Ecol 2022;59:300–13.
[98] Badenes-Pérez FR. Trap crops and insectary plants in the order Brassicales. Ann Entomol Soc Am 2018;112:318–29.
[99] Midega CAO, Pittchar JO, Pickett JA, Hailu GW, Khan ZR. A climate-adapted push-pull system effectively controls fall armyworm, *Spodoptera frugiperda* (J E Smith), in maize in East Africa. Crop Protect 2018;105:10–5.
[100] Thorbek P, Bilde T. Reduced numbers of generalist arthropod predators after crop management. J Appl Ecol 2004;41:526–38.
[101] Schaak H, Bommarco R, Hansson H, Kuns B, Nilsson P. Long-term trends in functional crop diversity across Swedish farms. Agric Ecosyst Environ 2023;343: 108269.
[102] Boiteau G, Picka JD, Watmough J. Potato field colonization by low-density populations of Colorado potato beetle as a function of crop rotation distance. J Econ Entomol 2008;101:1575–83.
[103] 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;58:507–17.
[104] Storkey J, Mead A, Addy J, MacDonald AJ. Agricultural intensification and climate change have increased the threat from weeds. Global Change Biol 2021;27: 2416–25.
[105] Kaspar TC, Singer JW. The use of cover crops to manage soil. In: Soil management: building a stable base for agriculture. John Wiley & Sons, Ltd; 2011. p. 321–37.
[106] Beaumelle L, Auriol A, Grasset M, Pavy A, Thiéry D, Rusch A. Benefits of increased cover crop diversity for predators and biological pest control depend on the landscape context. Ecol Solut Evid 2021;2:e12086.
[107] Lu Y, Wu K, Jiang Y, Guo Y, Desneux N. Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. Nature 2012;487:362–5.
[108] Bianchi FJJA. From pattern to process: towards mechanistic design principles for pest suppressive landscapes. Basic Appl Ecol 2022;64:157–71.
[109] Landis DA. Designing agricultural landscapes for biodiversity-based ecosystem services. Basic Appl Ecol 2017;18:1–12.
[110] Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, et al. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 2011;14:101–12.
[111] Perović D, Gámez-Virués S, Börschig C, Klein AM, Krauss J, Steckel J, et al. Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. J Appl Ecol 2015;52:505–13.
[112] van Schalkwyk J, Pryke JS, Samways MJ, Gaigher R. Spillover of terrestrial arthropod species and beta diversity in perennial crops relative to spatial scale of land-use intensity. J Appl Ecol 2020;57:1469–81.
[113] Tscharntke T, Grass I, Wanger TC, Westphal C, Batáry P. Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends Ecol Evol 2021;36:919–30.
[114] Monticelli LS, Bishop J, Desneux N, Gurr GM, Jaworski CC, McLean AHC, et al. Chapter Six - multiple global change impacts on parasitism and biocontrol services in future agricultural landscapes. In: Bohan DA, Dumbrell AJ, Vanbergen AJ, editors. The Future of agricultural landscapes, Part III, adv. Ecol. Res. Academic Press; 2021. p. 245–304.
[115] Bianchi FJJA, Booij CJH, Tscharntke T. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc Roy Soc B 2006;273:1715–27.
[116] Furlong MJ, Ang GCK, Silva R, Zalucki MP. Bringing ecology back: how can the chemistry of indirect plant defenses against herbivory be manipulated to improve pest management? Front Plant Sci 2018;9.
[117] Alignier A, Solé-Senan XO, Robleño I, Baraibar B, Fahrig L, Giralt D, et al. Configurational crop heterogeneity increases within-field plant diversity. J Appl Ecol 2020;57:654–63.
[118] Thomine E, Rusch A, Desneux N. Predators do not benefit from crop diversity but respond to configurational heterogeneity in wheat and cotton fields. Landsc Ecol 2023;38:439–47.
[119] Rand TA, Tylianakis JM, Tscharntke T. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecol Lett 2006;9:603–14.
[120] Sarthou JP, Badoz A, Vaissière B, Chevallier A, Rusch A. Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats. Agric Ecosyst Environ 2014;194:17–28.
[121] Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, et al. Landscape moderation of biodiversity patterns and processes-eight hypotheses. Biol Rev 2012;87:661–85.
[122] Aguilera G, Roslin T, Miller K, Tamburini G, Birkhofer K, Caballero-Lopez B, et al. Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. J Appl Ecol 2020;57:2170–9.

[123] Lichtenberg EM, Kennedy CM, Kremen C, Batáry P, Berendse F, Bommarco R, et al. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Global Change Biol 2017;23:4946–57.
[124] Fricke U, Redlich S, Zhang J, Benjamin CS, Englmeier J, Ganuza C, et al. Earlier flowering of winter oilseed rape compensates for higher pest pressure in warmer climates. J Appl Ecol 2023;60:365–75.
[125] Raderschall CA, Lundin O, Aguilera G, Lindström SAM, Bommarco R. Legacy of landscape crop diversity enhances carabid beetle species richness and promotes granivores. Agric Ecosyst Environ 2022;340:108191.
[126] Berdeni D, Turner A, Grayson RP, Llanos J, Holden J, Firbank LG, et al. Soil quality regeneration by grass-clover leys in arable rotations compared to permanent grassland: effects on wheat yield and resilience to drought and flooding. Soil Res 2021;212:105037.
[127] Guest EJ, Palfreeman LJ, Holden J, Chapman PJ, Firbank LG, Lappage MG, et al. Soil macroaggregation drives sequestration of organic carbon and nitrogen with three-year grass-clover leys in arable rotations. Sci Total Environ 2022;852: 158358.
[128] Dwivedi SL, van Bueren ETL, Ceccarelli S, Grando S, Upadhyaya HD, Ortiz R. Diversifying food systems in the pursuit of sustainable food production and healthy diets. Trends Plant Sci 2017;10:842–56.
[129] Degani E, Leigh SG, Barber HM, Jones HE, Lukac M, Sutton P, et al. Crop rotations in a climate change scenario: short-term effects of crop diversity on resilience and ecosystem service provision under drought. Agric Ecosyst Environ 2019;285: 106625.
[130] Vogel E, Donat MG, Alexander LV, Meinshausen M, Ray DK, Karoly D, et al. The effects of climate extremes on global agricultural yields. Environ Res Lett 2019;14: 054010.
[131] Birthal PS, Hazrana J. Crop diversification and resilience of agriculture to climatic shocks: evidence from India. Agric Syst 2019;173:345–54.
[132] Hatt S, Boeraeve F, Artru S, Dufrêne M, Francis F. Spatial diversification of agroecosystems to enhance biological control and other regulating services: an agroecological perspective. Sci Total Environ 2018;621:600–11.
[133] Maas B, Fabian Y, Kross SM, Richter A. Divergent farmer and scientist perceptions of agricultural biodiversity, ecosystem services and decision-making. Biol Conserv 2021;256:109065.
[134] Thomine E, Mumford J, Rusch A, Desneux N. Using crop diversity to lower pesticide use: socio-ecological approaches. Sci Total Environ 2022;804:150156.
[135] Van der Werf W, Bianchi F. Options for diversifying agricultural systems to reduce pesticide use: can we learn from nature? Outlook Agric 2022;51:105–13.
[136] Krzywoszynska A. Making knowledge and meaning in communities of practice: what role may science play? The case of sustainable soil management in England. Soil Use Manag 2019;35:160–8.
[137] Jaworski CC, Krzywoszynska A, Leake JR, Dicks LV. Sustainable soil management in the UK: a survey of current practices and how they relate to the principles of regenerative agriculture. Soil Use Manag; 2023.
[138] Sanchez AC, Kamau HN, Grazioli F, Jones SK. Financial profitability of diversified farming systems: a global meta-analysis. Ecol Econ 2022;201:107595.
[139] Vialatte A, Tibi A, Alignier A, Angeon V, Bedoussac L, Bohan DA, et al. Chapter Four - promoting crop pest control by plant diversification in agricultural landscapes: a conceptual framework for analysing feedback loops between agro-ecological and socio-economic effects. In: Bohan DA, Dumbrell AJ, Vanbergen AJ, editors. The Future of agricultural landscapes, Part III, adv. Ecol. Res. Academic Press; 2022. p. 133–65.
[140] Goucher L, Bruce R, Cameron DD, Koh LSC, Horton P. The environmental impact of fertilizer embodied in a wheat-to-bread supply chain. Nature Plants 2017;3: 17012.
[141] Lazzaro M, Costanzo A, Bàrberi P. Single vs multiple agroecosystem services provided by common wheat cultivar mixtures: weed suppression, grain yield and quality. Field Crop Res 2018;221:277–97.
[142] Ball BC, Bingham I, Rees RM, Watson CA, Litterick A. The role of crop rotations in determining soil structure and crop growth conditions. Can J Soil Sci 2005;85: 557–77.
[143] Shah F, Wu W. Soil and crop management strategies to ensure higher crop productivity within sustainable environments. Sustainability 2019;11.
[144] Narwal SS. Allelopathy in crop production. Scientific Publishers; 2012.
[145] Shekoofa A, Safikhan S, Raper TB, Butler SA. Allelopathic impacts of cover crop species and termination timing on cotton germination and seedling growth. Agronomy 2020;10:638.
[146] Li C, Hoffland E, Kuyper TW, Yu Y, Li H, Zhang C, et al. Yield gain, complementarity and competitive dominance in intercropping in China: a meta-analysis of drivers of yield gain using additive partitioning. Eur J Agron 2020;113: 125987.
[147] Tittonell P, Pineiro G, Garibaldi LA, Dogliotti S, Olff H, Jobaggy EG. Agroecology in large scale farming – a research agenda. Front Sustain Food Syst 2020;4: 584605.
[148] Meynard JM, Jeuffroy MH, Bail ML, Lefèvre A, Magrini MB, Michon C. Designing coupled innovations for the sustainability transition of agrifood systems. Agric Syst 2017;157:330–9.
[149] Duarte GT, Santos PM, Cornelissen TG, Ribeiro MC, Paglia AP. The effects of landscape patterns on ecosystem services: meta-analyses of landscape services. Landsc Ecol 2018;33:1247–57.
[150] Karp DS, Chaplin-Kramer R, Meehan TD, Martin EA, DeClerck F, Grab H, et al. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proc Natl Acad Sci USA 2018;115:E786–7870.