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Crop diversification to promote arthropod pest management: A review

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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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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 olfactory 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

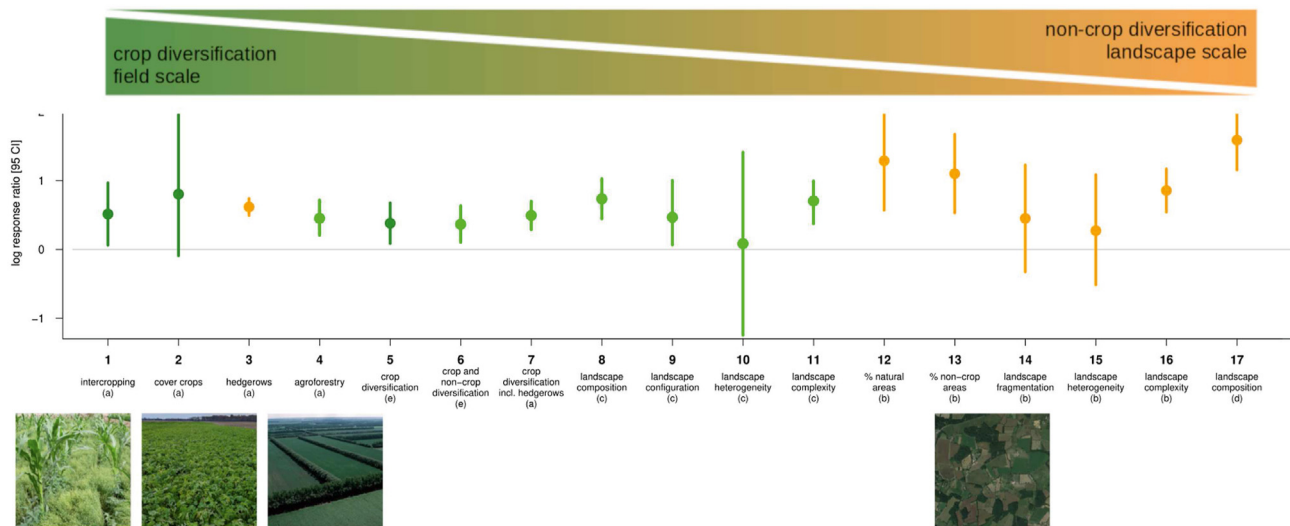


Fig. 1. Relative effect sizes (estimated median log of response ratio and 95% confidence interval) of crop and non-crop diversification measures on pest control metrics extracted from five meta-analyses: (a) (Beillouin et al., 2021 [85]); (b) (Tamburini et al., 2020 [21]); (c) (Estrada-Carmona et al., 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,
2			8	1948	cover crops	field, farm	crop	cover crops, grass strips	pest abundance, weed abundance,
3			2	13	hedgerows	local to landscape	non-crop	Hedgerows	other (natural enemy abundance, ...)
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
13				33	% non-crop areas	landscape	non-crop	percent non-crop areas	(abundance, richness, diversity, direct effect on pest reduction)
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 *Brachiaria* 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 validate 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

ND 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: ND reports financial support was provided by European Union.

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Authors' contributions

CCJ, ET and AR wrote the manuscript; AV, ND and SW contributed ideas and proofread the manuscript; ND secured funding. All authors agreed to co-author the manuscript.

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