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Review

Designing pest suppressive agroecosystems: Principles for an integrative diversification science

Séverin Hatt *, Thomas F. Döring

University of Bonn, Institute of Crop Science and Resource Conservation, Agroecology and Organic Farming group, Auf Dem Hügel 6, 53121 Bonn, Germany

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ABSTRACT

While many pesticides are detrimental to human health and the environment, drastically reducing their use and risks in agriculture has been set as a key target for global environmental policies. To this end, redesigning agroecosystems by increasing plant diversity at the cropping system and landscape levels is increasingly seen as imperative. Positive evidence that diversifying agroecosystems suppresses pests is accumulating and many ecological mechanisms driving pest suppression are known. Yet, variability in effects, risks of failure, and the limited adoption of diversification practices, call for improving diversification science. The overarching challenge lies in shifting from homogeneous production systems targeting yield at the cost of high input uses, to complex biodiversity-based environments resilient to pest pressure and delivering multifunctional performances. Therefore, a new conceptual umbrella to guide future agroecosystem design is proposed, which consists of integrating four principles: (i) embracing complexity, by jointly considering the multiple pests and their enemies; (ii) considering traits, in mobilizing the functional grammar; (iii) stacking diversification practices, by strategically combining the multiple facets of plant diversity at multiple scales; (iv) translating ecological processes into socio-economic benefits to adopt a multifunctional perspective. While addressing the associated implications for science and research, the present review critically discusses how to mobilize the spatio-temporal cross-scale dependencies of interactions in agroecosystems. Promoting synergies and building on the functional complementarities of ecological processes is proposed as a way to strengthen agroecosystem resilience to pest outbreaks.

1. Introduction

Agriculture is facing tremendous challenges to feed an increasing world population, without harming biodiversity, and while adapting to climate change. With the aim of producing more, conventional agriculture has intensified crop production systems with the use of synthesized inputs (Tilman et al., 2002), and by simplifying agricultural landscapes (e.g. Ihse, 1995). These practices, however, share responsibility in global warming (Mbow et al., 2019) and the loss of biodiversity (Gamez-Virués et al., 2015; Outhwaite et al., 2022). Through a negative feedback loop, the climate and biodiversity crises are now already beginning to challenge cropping systems' productive capacity by aggravating abiotic, but also biotic, stresses (Ortiz et al., 2021).

A critical threat lies in pests (i.e. insect herbivores, weed plants and pathogens of crop plants), for which management in conventional agriculture has largely relied on applying synthesized pesticides (Hossard et al., 2017; Tilman et al., 2002). Global warming is now expected to increase crop losses to insect pests (Deutsch et al., 2018) and diseases (Pautasso et al., 2012), and pesticide efficacy at controlling pests is expected to decline with climate change (Matzrafi, 2019). Pesticides, in addition, negatively affect the potential of natural regulation (i.e. biological control) offered by natural enemies (i.e. predators and parasitoids) (Geiger et al., 2010), whose abundance and diversity are generally declining along with the loss of biodiversity (Zhou et al., 2023).

Homogenous crop fields, and fields in simplified landscapes, are frequently and intensively treated with pesticides (Gagic et al., 2021; Meehan et al., 2011; Nicholson and Williams, 2021). They are sensitive to outbreaks of specialist pests and are poor in natural enemies, hence facing low effective biological control (Paredes et al., 2021; Rusch et al., 2016). While pesticides threaten natural enemies on the one hand (Pisa et al., 2021), pesticide efficacy at reducing pests may be significant only in the absence of natural enemies on the other hand (Janssen and van Rijn, 2021). Getting out of this pesticide treadmill requires to deeply redesign agroecosystems towards pest suppressive cropping systems and landscapes.

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* Corresponding author.
E-mail address: shatt@uni-bonn.de (S. Hatt).

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An agroecosystem associates a field and its margins, and is embedded in a broader landscape (Moonen and Bàrberi, 2008). It is made of planned and associated biodiversity, the former creating the conditions for the later to develop (Altieri, 1999). Planned biodiversity includes the crop plants and/or livestock raised at the field level, and the non-crop plants sown and managed at the field margins and at the broader landscape. Associated biodiversity – that can be found at the field, the margins, and the landscape level – is made of all the organisms that were not included on purpose. Some of them are harmful to the crops and the livestock: the spontaneous plants potentially competing with crops for resources (i.e. weeds), herbivores and disease-transmitting vectors (i.e. many insects), and bacteria, fungi and viruses responsible for diseases (i.e. pathogens) (Oerke, 2006). Others are beneficial, i.e. the natural enemies, that can be predators and parasitoids of insects and weeds, and beneficial micro-organisms (Wyckhuys et al., 2022). Redesigning agroecosystems for insect pest, disease and weed control can imply revisiting soil management strategies (Müller et al., 2022), integrating crop and livestock production (Clark and Gage, 1996), and diversifying the cropping systems and landscapes through increasing plant diversity over time and space within fields (on-site) and at their margins (off-site) (Lemaire et al., 2018). Diversifying – the focus of the present article – is especially a key strategy to maximize functional biodiversity, towards reducing the ability of pests to colonize crops and spread, and to favour biological control by natural enemies (Hatt et al., 2018a). Several diversification practices exist: rotating crops, cultivar mixtures, intercropping, companion planting, agroforestry, managing field margins (defined in Table 1).

As elaborated below, well-designed diversified agroecosystems significantly suppress pests. Ecological principles driving pest suppression in diversified agroecosystems have been described repeatedly (Andow, 1991; Bianchi et al., 2006; Boudreau, 2013; Petit et al., 2018; Plantegenest et al., 2007), and empirical evidence has been compiled in quantitative syntheses. This article briefly recalls these principles and summarizes this evidence, while aiming to pave the way forward. Indeed, despite overall positive impact at suppressing pests, variability in effects (Karp et al., 2018) and risks of failures (Tscharntke et al., 2016) remain; and overall, adoption of diversification practices by farmers has been limited. Beyond socio-technical barriers hindering the adoption of diversification practices (Meynard et al., 2018; Timaeus et al., 2022), research on diversification to enhance pest control has remained too fragmented in its scientific objects, methodological approaches, scale of implementation, and evaluation criteria. It is argued that for new agroecosystem design to substantially increase synergies and be more resilient, diversification science needs to adopt a more integrative perspective. Through a thorough analysis of the scientific literature, and building on the authors' experience as field-based experimenters, a new conceptual umbrella for an integrative diversification science is proposed, consisting of four principles: (i) *embracing complexity*, and considering pests and their natural enemies jointly because they generally occur simultaneously in fields and interact; (ii) *considering traits*, and adopt a stronger functional approach because the interactions between organisms depend on their respective morpho-physio-phenological attributes; (iii) *stacking diversification practices*, by strategically combining the multiple facets of plant diversity because complementary bottom-up and top-down effects are observed; (iv) *translating ecological processes into socio-economic benefits*, because for farmers, not only the ecological functioning matters, but also business and the opinion of society. The perspective in which the integration of these principles can enhance synergies and strengthen resilience to pest outbreaks is critically addressed. Finally, the implications for scientific research, and the capacity of this last point to effectively diversify crop production systems, are discussed.

2. Diversifying to suppress pests

The impact of cropping system and landscape diversification on insect pests, weeds and diseases and their regulation by natural enemies has been extensively studied. Knowledge on the underlying ecological mechanisms and the quantitative evidence that increasing plant diversity reduces pests in general is summarized. Recalling this knowledge allows identifying room for improvement to design pest suppressive agroecosystems.

Table 1
Definitions of key diversification practices.

Practice	Brief description
Rotation	"Growing different crops in systematic and recurring sequence on the same land, as compared to monoculture, in which a particular crop is planted repeatedly in the same field" (Liebman and Dyck, 1993). Rotations range from very simple alternations of two crop species (e.g. maize-soybean or rice-wheat) to complex succession of several crops including for instance cereals, legumes, oilseed crops, and tuber crops. They may include winter cover crops to bridge harvest in summer and next sowing in spring, and temporal grasslands grazed or harvested in integrated crop-livestock systems.
Cultivar mixtures	"The simultaneous cultivation of multiple cultivars of the same species" (Reiss and Drinkwater, 2018). It can involve two to many cultivars being mixed. A similar approach of intraspecific (i.e. genetic) diversification is the use of composite cross populations (Döring et al., 2011).
Intercropping	Growing together two or more cash crop species at least for a time. Species can be mixed or associated in rows or strips of various width. Relay intercropping implies a time shift in the sowing and harvest of the associated crops. Identity, proximity (high in mixture, low in strip intercropping) and the relative density of the intercropped species are key parameters determining intercropping performances (Li et al., 2020).
Companion planting	Growing a cash crop with one or more plants that are not harvested. Companion plants can be preestablished as a living mulch, sown with the cash crop, or later on in relay (Verret et al., 2017).
Agroforestry	"The deliberate integration of trees with agricultural crops and/or livestock either simultaneously or sequentially on the same unit of land" (Mosquera-Losada et al., 2009). Agroforestry systems are classified notably according to their associated components (trees and crops and/or livestock) and their spatio-temporal arrangement (i.e. from densely mixed to sparse and aligned) (McAdam et al., 2009).
Field margin management	Managing and conserving "the whole of the crop edge, any margin strip present and the semi-natural habitat associated with the boundary" (Marshall and Moonen, 2002). Boundaries are the outer limits of the field, and are typically a hedge, fence or wall, with potential herbaceous vegetation, and any associated watercourse. Margin strips are established between the crop and the boundaries, and are typically grassy or flowering strips. Sown strips can largely differ from their species composition (e.g. forb/grass ratio), richness (mono- vs. pluri-specific incl. tens of species), perenniality (annual vs. pluriannual).

2.1. Why does it work

Diversifying crop sequences through time is an ancient practice (White, 1970). Alternating crop species of different families and cultivation seasons generates an offset between pests' life cycle and the crops, which limits the building-up of pest populations (Francis, 2005). Variations in field disturbance caused by preparation works (ploughing, seed bed preparation) especially affect weed populations by disrupting their growth and development and prevent that only few species dominate in the weed flora (Liebman and Dyck, 1993). In space, diluting pests' host plants within non-host ones creates physical barriers affecting insect (Finch and Collier, 2012; Mansion-Vaquié et al., 2020) as well as disease (Zhu et al., 2000) capacity to spread. It modifies visual contrasts used by insects to locate their host plants (Döring, 2014; Döring and Röhrig, 2016), and changes micro-climate, wind, and splash from rain drops involved in pathogen dispersion (Boudreau, 2013). Increasing sown plant diversity strengthens the competition for light, nutrient and water resources and eventually leave fewer opportunities for weeds to establish and grow (Petit et al., 2018). Aside crop fields, field margins favour the conservation of natural enemies controlling pests (Gurr et al., 2017). In annual cropping systems facing high disturbances, field margins represent stable (Tooker et al., 2020) and continuous (Iuliano and Gratton, 2020) trophic and structural resources that are essential for natural enemies to accomplish their life cycle. Pluriannual non-crop habitats are overwintering sites (Ganser et al., 2019) and provide essential and alternative food, such as pollen and nectar that are key resources increasing fitness of several natural enemies, e.g. predatory hoverflies (Syrphidae) (Van Rijn and Wäckers, 2016), lacewings (Chrysopidae) (Resende et al., 2017), ladybird beetles (Coccinellidae) (Hatt and Osawa, 2019a) and parasitoid wasps (Lu et al., 2014). Hence, at a broader scale as well, semi-natural habitats in the landscape provide trophic and structural resources for natural enemies of pests (Begg et al., 2017). Since different natural enemy taxa respond differently to habitat types (Labruyere et al., 2016; Lefebvre et al., 2016; Sarthou et al., 2005), a diversity of habitats is necessary at the landscape level to support the diversity of pest natural enemies (Holland et al., 2016). Finally, a heterogeneous configuration of the landscape, leading to a high density of edges, allows natural enemies overwintering in semi-natural habitats to spill over into crop fields and control pests (Martin et al., 2019). A diversity of habitats in the landscape also reduces disease infection, by diluting hosts and acting as barriers to pathogen spread, although corridors and edges can also favour pathogen dispersion (Plantegenest et al., 2007). As for weeds, the diversity of habitats in complex landscapes increases the pool of plant diversity potentially spilling over to the cultivated fields. On the one hand, diversity of non-crop habitats can result in increasing the diversity of in-field weed communities and reducing the abundance of aggressive and highly problematic species (Petit et al., 2011; Roschewitz et al., 2005), *in fine* mitigating weed impact on crop yield (Adeux et al., 2019). On the other hand, non-crop habitats at field margins can represent refugia for plant diversity without increasing weed pressure in the centre of the field (Cordeau et al., 2012; Marshall, 2009).

2.2. *Evidence that it works*

Effects of diversification on pest control were synthesized in quantitative reviews published over the last decade. They show that at the field and farm scales, increasing plant diversity within fields and at margins significantly reduces herbivores and their damages on crops and increases their natural enemies (Letourneau et al., 2011; Wan et al., 2020). At the field scale specifically, the abundance of generalist predators increases while the abundance of specialist herbivores decreases when plant diversity increases (Dassou and Tixier, 2016). When considering certain diversification practices specifically, wildflower strips at field margins enhance insect pest control by 16 % in the adjacent crops (Albrecht et al., 2021). Intercropping a cash crop with a legume companion plant reduces weed biomass by 42–56 % without reducing crop yield (Verret et al., 2017). Intercropping two cash crops reduces weed biomass by 58 % on average in comparison to the less weed competitive crop species grown as sole crop (Gu et al., 2021). Intercropping cereals with legumes reduces disease incidence by 45 % on average (Zhang et al., 2019). A vote counting analysis found a significant number of cases (81 %) reporting a significant reduction of herbivores in wheat (*Triticum aestivum* L., Poaceae)-based intercropping systems compared to sole-cropping, but inconsistent effects were found on their natural enemies (Lopes et al., 2016). Agroforestry generally allows to reduce weed abundance, but a significant reduction of insect pests and diseases was only found in agroforestry systems involving perennial crops (Pumariño et al., 2015). Diversifying crop rotations allows reducing weed density by 49 % on average, but no significant effect was found on weed biomass (Weisberger et al., 2019). At the landscape scale, landscapes with higher proportions of semi-natural areas have lower insect pest abundance or higher insect pest control in fields (Veres et al., 2013). Notably, aphid (Hemiptera: Aphididae) control linearly decreases when the proportion of cultivated land increases (i.e. when the proportion of semi-natural habitats decreases) and was found to be 46 % lower in homogeneous than complex landscapes (Rusch et al., 2016). Chaplin-Kramer et al. (2011) however did not find an effect of landscape complexity on pest abundance although at the same time reported a strong positive effect at increasing natural enemy diversity. By disentangling the cascading effects of landscape complexity on pest control, Dainese et al. (2019) showed that pest control relies on natural enemy richness, which is however negatively affected by landscape simplification. Finally, among a pool of 750 species of natural enemies, 44 % of species reach highest abundances in landscapes with high edge density (i.e. high configurational heterogeneity) while at the same time edge density improves pest control by 1.4-fold (Martin et al., 2019). Duarte et al. (2018) found that landscape complexity (i.e. areas with higher percentages of natural habitats) can increase disease control up to 20 %. While there are several studies that show weed diversity is higher in fields embedded in diversified landscapes (e.g. Gaba et al., 2010; Roschewitz et al., 2005), quantitative reviews summarizing the effects of landscape complexity on weed pressure and diversity are currently missing.

2.3. *Room for improvement*

Despite these significant positive effects, diversification practices remain poorly adopted by farmers. Suppressing pests through biodiversity-based approaches rather than by spraying pesticides is perceived as complex from an ecological perspective, and challenging from a technical point of view (Kleijn et al., 2019; Timaeus et al., 2022). For many farmers, the overall significant positive effects found in quantitative syntheses may not be convincing enough when variability in effects (Karp et al., 2018) and even risks of failures (Tscharntke et al., 2016) remain. Consequently, relying on regulating processes in agroecosystems to control pests is perceived as risky (Salliou and Barnaud, 2017). This may explain why pesticide-based plant protection remains the norm (Hossard et al., 2017), even in Integrated Pest Management (IPM) (Deguine et al., 2021) where using pesticides should be considered as a last resort (Stenberg, 2017).

For addressing the problem of variable effects and low adoption it is argued that diversification science needs to build on a better basis; first, through a better integration of its research objects: while research on diversification has been increasingly considering the diversity of pests and enemies occurring simultaneously in fields (i.e. insects, weeds, pathogens) (Baniszewski et al., 2021; Ratnadass et al., 2021), few are assessing their interactions (Serée et al., 2023) and the resulting synergies or trade-offs in their joint management (Tamburini et al., 2016). Second, through a better integration of its methodological approaches: by considering biological diversity mostly through a taxonomic perspective, studies on diversification have been producing results that very much depend on species identity (Hatt et al., 2019b). Although useful for practical applications, research would highly gain from adopting a more functional approach, which handles interactions through organisms' traits. Mechanisms could then be described beyond species identity (Cadotte et al., 2011), rendering findings more general (Gardarin et al., 2018; Perovic et al., 2018). Third, through a better integration of the variety of diversification practices: each diversification practice taken separately allows to partially reduce pest pressure (see section above) but the absolute effect, although significant, might not be sufficient to fully protect crops against pests (Romeis et al., 2019; Torres and Bueno, 2018). Although an array of diversification practices affect both insects, weeds and pathogens (i.e. crop rotation, intercropping, agroforestry, companion planting) (Kremen and Miles, 2012; and section above), the synergistic effects of stacking them remain poorly studied (Ditzler et al., 2021; Juventia et al., 2021). Fourth, through a better integration of the evaluation criteria: most studies on diversification for pest suppression evaluate the impact on pest reduction, and crop damage when it is relevant (e.g. for fresh-marketed products). Effects on crop productivity remain limited for some diversification techniques (e.g. field margin management, Albrecht et al., 2021) and economic and societal evaluations are scarce. More importantly, experimental studies rarely address both the impact on pest control and socio-economic performances of diversification (Vialatte et al., 2022; but see Gurr et al., 2016).

3. Principles for an integrative diversification science

Four principles are proposed with the aim of improving the science base when designing pest suppressive agroecosystems. While each principle addresses one of the issues identified above (section 2.3), they constitute the basis for an integrative diversification science.

3.1. Embracing complexity

Multiple organisms in agroecosystems potentially affect crop yield and quality, either positively through the delivery of ecosystem services, or negatively when they are responsible for ecosystem disservices (Gillespie and Wratten, 2017; Zhang et al., 2007). While these organisms interact and potentially regulate each other, it is necessary to consider them jointly and assess the net positive/negative effects, needed to guide management decisions. Some insect pests feeding on plant resources transmit viruses responsible for important yield loss (e.g. Hemipteran like aphids) (Williams and Dixon, 2007). Their regulation should simultaneously reduce direct damages caused by feeding, and indirect damages caused by the viruses. Diversification of tobacco (*Nicotiana tabacum* L., Solanaceae) cropping through cultivar mixtures (variety mixtures) was shown to reduce the abundance of the green peach aphid (*Myzus persicae* Sulzer), as well as the incidence and severity of the Tobacco Mosaic Virus it transmits (Lai et al., 2017). Regulation of insect pests can be mediated by natural enemies, nonetheless natural enemies can trigger anti-predation or anti-parasitism behaviour leading to pest dispersion and consequently to virus spreading. Dáder et al. (2012) showed in the case of the aphid *Aphis gossypii* Glover facing parasitism, that although the parasitoid *Aphidius colemani* (Viereck) (Hymenoptera: Braconidae) favoured the dispersion of the Cucumber Mosaic Virus and the Cucurbit Aphid-borne Yellow Virus in the short-term, virus incidence was reduced by the control of aphid abundance in the long term.

In the insect-pathogen system, weeds can have dual effects as they closely interact with disease inocula and populations of animal pests and natural enemies (Barbercheck and Wallace, 2021; Franke et al., 2009). Indeed weeds, in addition to their potential competition for resources against crops, can be alternative hosts of pathogens and food sources for animal pests. However, weed cover can also positively affect predatory invertebrates (Fig. 1a) (Smith et al., 2020), notably the density and activity of carabid beetles (Coleoptera: Carabidae) (Diehl et al., 2012). Flowering weeds can also attract and benefit flower visiting natural enemies (Fig. 1 b-f) (Altieri and Nicholls, 2004; Norris and Kogan, 2000). Finally, some weed species can host non-pest insects being (or producing) alternative resources for natural enemies. For instance, DiTommaso et al. (2016) highlighted how the common milkweed (*Asclepias syriaca* L., Apocynaceae), although a competitor against maize, facilitates the parasitism of the corn borer (*Ostrinia nubilalis* Hübner, Lepidoptera: Crambidae) by supporting aphid-produced honeydew benefiting to the corn borer parasitoid *Trichogramma ostriniae* Peng and Chen (Hymenoptera: Trichogrammatidae).

In this context, Storkey and Westbury (2007) asked whether there is "such a thing as a 'good weed'?", and defined a beneficial weed as "a

Fig. 1. Predatory insects on weeds: ladybird beetles on (a) weed vegetation nearby faba bean (*Vicia faba* L.), (b) on black-bindweed (*Fallopia convolvulus* (L.) Á.Löve) looking for alternative aphid prey, and (c) on mustard (*Sinapis arvensis* L.) flower bud; lacewings (*Chrysoperla carnea* Stephens) on (d) chamomille (*Matricaria recutita* L.), and (e) poppy (*Papaver rhoeas* L.); (f) a hoverfly on *F. convolvulus* flower. (Photos: S. Hatt).

species that provides low levels of competition with the crop and has potential value as a resource for higher trophic groups." Eighteen weed species were classified as "with biodiversity value" (i.e. benefiting natural enemy insects and birds) and with intermediate or low competitive ability with winter wheat in the context of UK (Storkey, 2006; Storkey and Westbury, 2007). The list includes for example the chickweed *Stellaria media* L. (Caryophyllaceae), the groundsel *Senecio vulgaris* L. (Asteraceae) or the annual meadow grass *Poa annua* L. (Poaceae). The same authors classified thirteen other species as "pernicious weeds that must be controlled," including the creeping thistle *Cirsium arvense* L. (Asteraceae) and the bitter dock *Rumex obtusifolius* L. (Polygonaceae). As some weed species can be desirable in agroecosystems, it was proposed to maintain a 10%-cover with such desirable weed species within crops (winter wheat) to support populations of higher trophic groups and related ecosystem services such as biological pest control (Smith et al., 2020). By attracting and supporting natural enemies within crops, weeds can be a key tool for conservation biological control, by getting the natural enemies close to the pests, i.e. their prey or host (Serée et al., 2023). In addition, the presence of weeds within crops would enhance plant diversity and could participate in diluting host plants and reducing risks of infection by pathogens and colonization by insect pests (Gunton, 2011).

Like weeds which can play a role in the control of insect pests and diseases, the presence of some insect pests can play an important role in the regulation of diseases. In shaded-coffee (*Coffea* sp. L., Rubiaceae) agroecosystems in Central America, a relatively high abundance of green coffee scales (*Coccus viridis* (Green), Hemiptera: Coccidae) allows the development of its natural enemy, the white halo fungus (*Lecanicillium lecanii*), this last being also a mycoparasite of the fungus *Hemileia vastatrix* responsible for the coffee leaf rust disease (Vandermeer et al., 2009, 2019). While green coffee scales are able to build large enough populations thanks to the protective action of ants (*Azteca instabilis* (Smith), Hymenoptera: Formicidae), they are not critical pests for the coffee plants since the associated built-up of the white halo fungus regularly eradicate them (Vandermeer et al., 2019). However, the development of *L. lecanii*, thanks to the mutualistic relation between *Azteca* ants and the green coffee scales, allows to partially maintain the coffee leaf rust disease at a moderate level (Jackson et al., 2012) (although other factors such as landscape effects have led to coffee rust disease outbreaks in the past, Avelino et al., 2012).

Through these examples, and in the continuity of Storkey and Westbury (2007), it can be asked whether there is such a thing as a "good pest"? Although pests are by definition harmful (Oerke, 2006), they can also be helpful. Helpful 'pests' would be those providing more benefits than damages, being more allies than threats, delivering more services than disservices, depending on context. Making such a distinction between helpful and harmful pests, however, represents a costly informational challenge: first, the helpful/harmful status of a given pest is likely to be density-dependent, as the density of the pest determines the level of damages on crops, but also triggers the development of its natural enemies (e.g. DiTommaso et al., 2016); second, the helpful/harmful status of a pest would depend on the combination of several of its traits and their net effects on ecosystem (dis)service (Yvoz et al., 2021), however variable across ecological conditions due to the inherent intraspecific plasticity of functional traits (Yvoz et al., 2020).

3.2. Considering traits

Assessing whether a given organism can provide benefits for agricultural production necessitates to understand how plants, animals, and micro-organisms interact in agroecosystems and how such interactions are translated into regulating processes. Considering organisms' traits, in addition to their taxonomic identity, can provide valuable understanding of the mechanisms underlying ecosystem processes (Cadotte et al., 2011). Applying, in pest science, theories and methods developed by functional ecology is promising to understand the effect of management strategies on pests and their natural enemies (Perovic et al., 2018), and to design pest suppressive diversified agroecosystems (Table 2; Gaba et al., 2014).

Organism' traits have been classified in two types: (i) response traits, that are those associated with the response of organisms to environmental factors; and (ii) effect traits, that are those affecting ecosystem functioning (Lavorel and Garnier, 2002). Single response or effect traits in a community can be studied by considering their community-weighted mean (CWM) and their functional divergence (FDvar). For a given trait, CWM is the mean of trait values weighted by the relative abundance of taxa bearing each value (Lavorel et al., 2008), while FDvar is the variance of trait values weighted by the abundance of each taxon in the community (Mason et al., 2003). The response/effect of multiple traits is captured by their functional diversity, that assesses the "distribution of traits in a community or the relative magnitude of species similarities and differences" (Cadotte et al., 2011). Among several available indices measuring functional diversity (Pla et al., 2012), functional dispersion (FDis) and Rao's quadratic entropy (Rao's Q) quantify the dispersion of species in the trait space weighted by their relative abundances. Being highly correlated to each other, FDis calculates the mean distance of individual species to the centroid of all species in the community while Rao's Q calculates the mean distance between two randomly selected individuals (Laliberté and Legendre, 2010).

Considering response traits of pests and their natural enemies can help understanding effects of agroecosystem diversification on functional biodiversity (Fig. 2). Comparisons of sole cropping (of wheat and oilseed rape (*Brassica napus* L., Brassicaceae)) with agroforestry systems showed that diversification favoured weed plants with competitive traits (i.e. perenniality, creeping habit, late and brief flowering) typical from less disturbed environments, herbivore and natural enemy invertebrates with a poor ability to disperse, and herbivores with specialist diets (Staton et al., 2021). Wheat fields with wildflower strips at margins hosted more spiders with active hunting strategies while fields without wildflower strips favoured more web-builder species (Gallé et al., 2020). Smaller fields (of about 3 ha on average, i.e. embedded in more diversified landscapes) promoted smaller and more carnivorous carabid species compared to larger fields (of about 18 ha on average) (Gallé et al., 2019). Assessing the effect of diversification practices on response traits furthermore informs on eventual cascading pest regulation processes since response traits are potentially linked with effect traits (Lavorel and Garnier, 2002; Perovic et al., 2018). Diet specialization obviously indicates whether a certain arthropod is a sap-sucker, an insect predator or a seed feeder, or both (e.g. Brooks et al., 2012). Body size can affect level of predation (Rusch et al., 2015). Dispersal ability, often correlated with body size in arthropods (Boetzl et al., 2019; Greenleaf et al., 2007), informs on the ability to spill over from semi-natural habitats into crops, affecting crop infestation by pests but also pest regulation by natural enemies (Pecheur et al., 2020; Staton et al., 2021). Hence, considering functional biodiversity through the lens of the response-effect model can lead to applying management strategies favouring species that do not adversely affect crops, and/or enhancing pest regulation.

Considering traits can also be used to design agroecosystems (Fig. 2). Knowledge on plant effect traits can be originally used to identify the plant species (i.e. crops but also weeds) that will directly and indirectly enhance pest regulating services (Hatt et al., 2019b; Navas, 2012), and can be applied to engineer diversified cropping (Storkey et al., 2015) and non-crop habitats (Hatt et al., 2020). Early biomass and allelopathic activity were identified as key plant traits determining plant competitiveness against other plants (Bertholdsson, 2005). Flower morphology, size and effective depth, blooming period, and flower height are among floral traits significantly affecting the attractivity and fitness of flower visiting insects (Fiedler and Landis, 2007; Van Rijn and Wäckers, 2016). In practice, Apiaceae species (e.g. *Coriandrum sativum* L., *Foeniculum vulgare* Mill., *Anethum graveolens* L.), but also *Centaurea cyanus* L. (Asteraceae) and *Vicia sativa* L. (Fabaceae), can be sown (or preserved if

Table 2
Selection of recent studies assessing the effect of agroecosystem diversification on weeds, insect pests and/or their natural enemies using functional metrics.[a]

Diversification approach	Agroecosystem compartment	Organisms	Metrics	Trait type (Response; Effect)	References
Companion planting	Crop	Weeds	Community Weighted Mean (CWM)	Response	Ciaccia et al. (2020)
Agroforestry	Crop	Weeds, Insect herbivores, Insect natural enemies	Functional dispersion (Rao's Q)	Response	Staton et al. (2021)
	Understory vegetation strip; Crop	Spiders, Carabids	Functional divergence (FDvar); Community Weighted Mean (CWM)	Response	Boinot et al. (2019b, 2020)
	Understory vegetation strip; Crop	Weeds	Functional composition	Response	Boinot et al. (2019a)
Field margin management	Wildflower strip	Forbs	Functional dispersion (Rao's Q)	Effect	Hatt et al. (2017)
	Wildflower strip	Forbs	Functional dispersion (FDis)	Effect	Gardarin et al. (2021)
	Wildflower strip	Forbs	Community Weighted Mean (CWM)	Effect	Hatt et al. (2019b, 2018b)
	Hedgerow, grassy strip, wildflower strip; Crop	Carabids	Functional dispersion (FDis); Community Weighted Mean (CWM)	Response	Pecheur et al. (2020)
	Crop	Spiders, Carabids	Functional divergence (FDvar); Community Weighted Mean (CWM)	Response	Gallé et al. (2020)
Landscape heterogeneity (small vs. large field)	Crop	Spiders, Carabids	Functional divergence (FDvar); Community Weighted Mean (CWM)	Response	Gallé et al. (2020, 2019)

[a] CWM is the mean of trait values weighted by the relative abundance of taxa bearing each value (Lavorel et al., 2008). FDvar is the variance of trait values weighted by the abundance of each taxa in the community (Mason et al., 2003). Functional dispersion (FDis) and Rao's quadratic entropy (Rao's Q) quantify the dispersion of species in the trait space weighted by their relative abundances (Laliberté and Legendre, 2010).

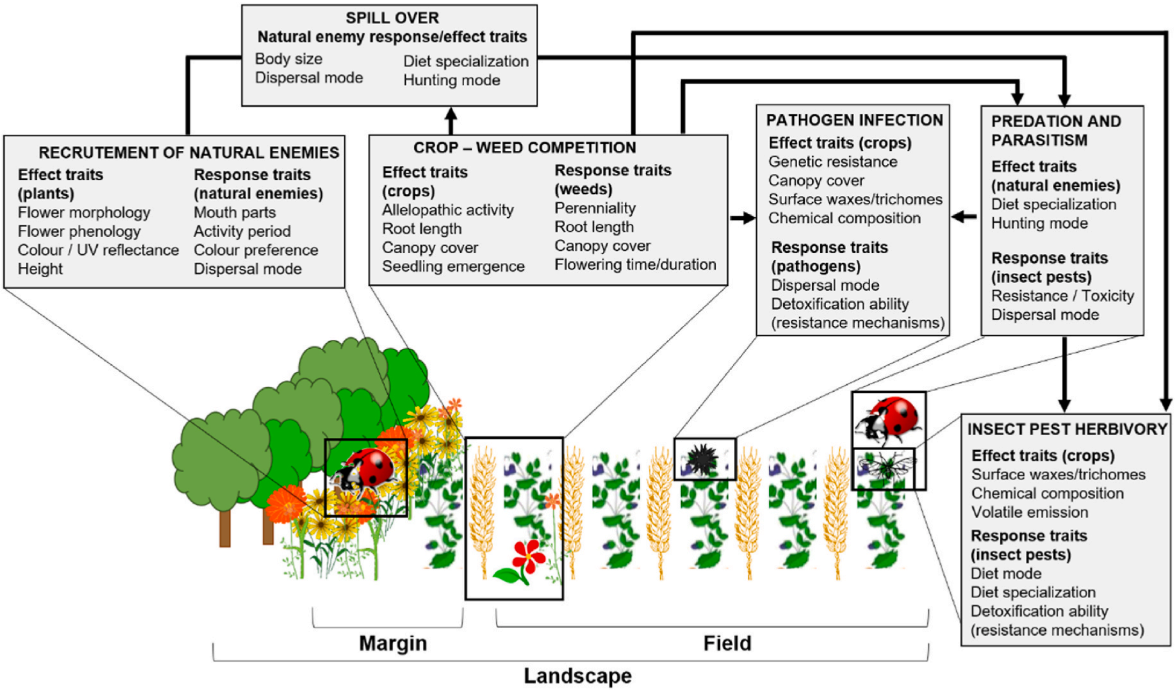

Fig. 2. Pest regulation processes as a function of key effect and response traits of plants, natural enemies and pests (insects, weeds and pathogens) in relation to field, their margins, and landscape diversification. Arrows indicate the relationships between the ecological processes, and hence the intersections of effect and response traits that potentially occur across spatial scales.

occurring as weed) to support predatory insects with short mouth parts (e.g. hoverflies, lacewings, ladybird beetles) thanks to their accessible nectar related to their reduced corolla depth and extra-floral nectar, respectively (e.g. Tschumi et al., 2016b). Alsike clover (*Trifolium hybridum* L., Fabaceae) and black medic (*Medicago lupulina* L., Fabacae) can be used as cover crops or companion plants to control weeds thanks to their rapid growth rate and allelopathic effect, respectively (Elsalahy et al., 2019). Barley (*Hordeum vulgare* L., Poaceae), harboring both a high early vigor and a high allelopathic activity (Bertholdsson, 2005), can be cultivated in association with poor weed competitive crops (e.g. pea (*Pisum sativum* L., Fabaceae)) to reduce weed presence (Corre-Hellou et al., 2011).

The studies that identified the plant effect traits useful to enhance pest regulating processes have often used monospecific plantings (e.g.

Fiedler and Landis, 2007) or even artificial devices (e.g. Sutherland et al., 1999). Nonetheless, in the case plant species are mixed, it becomes necessary to understand how the relative abundance of different traits and their value (dis)similarities affect ecological processes. Research on wildflower mixtures sown to support natural enemies of insect pests found that a higher dissimilarity in trait values between the mixed species (i.e. higher functional diversity) does not attract and support a higher abundance and diversity of aphid predators (Hatt et al., 2017); and instead showed that the abundance of natural enemies is driven by the relative abundance of certain trait values (i.e. community weighted mean of some traits). In particular, it was observed that parasitoids of pollen beetles (*Meligethes* spp. Stephens, Coleoptera: Nitidulidae) were more abundant in mixtures with yellow flowers and flowers with peripherical corolla parts reflecting ultra-violet (Hatt et al., 2018b), the lacewing *Chrysoperla carnae* Stephens and the ladybird beetles *Harmonia axyridis* Pallas and *Propylea quatuordecimpuctata* Linnaeus were more abundant in mixtures with flowers harbouring an ultra-violet pattern, the hoverflies *Episyrphus balteatus* De Geer and *Eupeodes corollae* Fabricius were more abundant in mixtures with open-nectar flowers (Hatt et al., 2019a).

When it comes to designing plant mixtures to enhance the natural regulation of pests, individual species known to compete against pests or known to favour pest natural enemies can be associated. This 'pick-and-mix' approach (Wäckers and Van Rijn, 2012) showed its effectiveness in the case of wildflower strips sown at field margins to enhance conservation biological control (Tschumi et al., 2015, 2016b). Plant species harbouring useful traits could also be associated to design a mixture that, as a whole, would showcase a relative abundance of trait values positively affecting pest regulation. This 'tailored functional diversity' approach (Hatt et al., 2020) nonetheless throws up new questions: what is the set of traits that must be considered? How many plant species harboring the same trait values but also different trait values should be mixed? What would be the right balance between trait diversity and redundancy?

3.3. *Stacking diversification practices*

Arranging and managing plant diversity has been the basis of agroecological engineering for new agroecosystem design (Gurr et al., 2004). Nonetheless so far, research on diversification has been focusing on one or the other component of the agroecosystem, e.g. intercropping for the crop field (Hufnagel et al., 2020) or wildflower strips for the margins (Hatt et al., 2020), and rarely attempted to combine different diversification practices. It can be hypothesised that "stacking diversity" through combining the various spatial and temporal diversification practices will strengthen their effects on pest regulation (Hokkanen, 2017).

A three-dimensional diversity approach was proposed, consisting of combining long-term rotations (temporal diversity) with species intercropping (spatial diversity) and cultivar mixtures (genetic diversity) (Ditzler et al., 2021). Empirical evidence was provided for two of the three dimensions (i.e. intercropping associated to cultivar mixtures). On the one hand, Ditzler et al. (2021) showed that combining strip intercropping (potato (*Solanum tuberosum* L., Solanaceae)-spring wheat) with cultivar mixtures (three different potato cultivars) significantly lowered the spread rate of the late blight disease (caused by *Phytophthora infestans* (Mont.) de Bary) on potato compared to intercropping alone and sole cropping. On the other hand, the same study reported that associating intercropping (wheat-faba bean (*Vicia faba* L., Fabaceae)) with cultivar mixtures of both species did not enhance the activity density, richness and evenness of aphid natural enemies, when compared to intercropping alone. Another study with cabbage (*Brassica oleracea* L., Brassicaceae) as the focus crop tested various crop and non-crop combinations in strip intercropping designs, and in some cases with crop cultivar mixtures (Juventia et al., 2021). Interestingly, non-crop features such as wildflower strips and grass-clover mixtures were associated in some strip intercropping designs. A key finding was that, across locations and designs, feeding injuries on cabbage leaves were significantly reduced as plant diversity within 15 m radius of cabbage strip increased (Juventia et al., 2021). This suggests that increasing plant diversity at the field scale beyond two cultivars or species (i.e. intercropping), or sole cropping with flower strips at margins, do indeed further enhance pest regulation.

These recent studies support the hypothesis that key synergies will arise from complex designs associating various diversification practices, including diversified cropping and the implementation of non-crop habitats. The strategic integration of these processes should lead to mobilizing five-dimensional diversity in new agroecosystem designs. Following the path opened by Ditzler et al. (2021) and Juventia et al. (2021), five-dimensional diversity would take advantage of a three-dimensional crop diversity (i.e. rotation, cultivar mixtures, and species intercropping) with a two-dimensional non-crop diversity (i.e. direct field margin, and surrounding landscape management) (Fig. 3). Nonetheless, this raises new challenges. First, implementing a five-dimensional diversification would have to deal with different spatio-temporal scales. Especially, the two dimensions of non-crop diversity are managed at different spatial scales, with direct field margins implemented at the farm level, and landscape diversity handled at the regional level. Hence, mobilizing four-dimensional diversity (i.e. rotation, cultivar mixtures, species intercropping, and direct field margin management) is in each farmer's hands; realising five-dimensional diversity necessitates organising stakeholders beyond farms' borders (Hatt et al., 2018a; Landis, 2017). Second, for experimental research, testing such multidimensional diversification is not trivial, because factorial experiments combining different factors of diversification are forbiddingly large and complex, while simpler trials testing the performance of a single stacked diversification treatment against current practice may fail to attribute observed effects to the components of diversification. Solutions may lie in the use of modelling (Bonato et al., 2023), from which predictions allow building scenarios that can be compared by varying key parameters, e.g. the proportion of non-crop habitats in a landscape (Ekroos et al., 2014) or the crop species to include in rotations or mixtures (Colbach et al., 2021). Yet, trade-offs between realistic predictions and generalization across systems occur as modelled systems complexify (Alexandridis et al., 2021). Using archetypes of ecological responses, defined as ecological phenomena showing similar responses to land-use change across different contexts and explained by similar trait-mediated processes, has been recently proposed to develop "mechanistic models of intermediate generality" (Alexandridis et al., 2022). Other developing pathways involve the collection of "big data" facilitated by the use of automated sensing technologies, and analyzed through machine learning algorithms (Høye et al., 2021).

3.4. *Translating ecological processes into socio-economic benefits*

Positive socio-economic benefits can arise from the diversification of agroecosystems. A recent meta-analysis showed that diversified farming systems are at least as profitable as simplified ones, and highlighted that total costs, gross income and profits are higher on average in diversified than in simplified systems, while the benefit-cost ratio are equivalent (Sánchez et al., 2022). Pesticide use could be reduced without any effect on productivity and profitability (e.g. 30–60% in France, Lechenet et al., 2017). In diversified agroecosystems, reducing pesticide usages enhances the natural regulation of insect pests (Geiger et al., 2010), which participates in maintaining productivity. Experiments conducted in rice agroecosystems showed that managing rice field bunds with non-rice crops (e.g. sesame *Sesamum indicum* L., Pedaliaceae (Gurr et al., 2016), mung bean *Vigna radiata* (L.) R. Wilczek, Fabaceae (Sattler et al., 2021)) allows reducing or avoiding insecticide applications while maintaining rice yield and increasing total income (e.g. +7.5% or US \$215 ha^{-1}, Gurr et al., 2016). Wildflower strips sown adjacent to organic vegetable greenhouses significantly reduced bio-insecticide applications

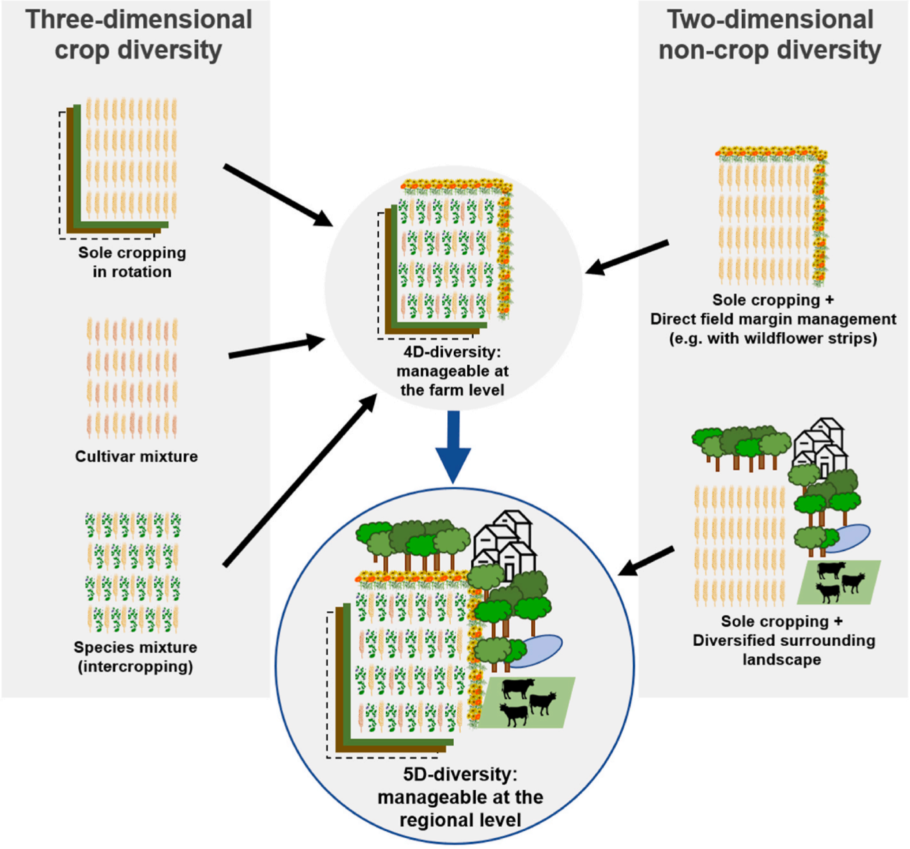

Fig. 3. Stacking diversification practices: towards a five-dimensional diversity taking advantage of a three-dimensional crop diversity (i.e. rotation, cultivar mixtures, and species intercropping) with a two-dimensional non-crop diversity (i.e. direct field margin, and surrounding landscape management).

(−34%) while eggplant (*Solanum melongena* L., Solanaceae) yield was maintained (Li et al., 2021). Infestation of insect pests was delayed in cotton (*Gossypium hirsutum* L., Malvaceae) cultivated in smaller fields and embedded in more diverse landscapes, leading to reduced insecticide applications, and resulting in higher yield (Gagic et al., 2021).

While diversifying would not reduce profitability, increasing crop diversity and reducing input usages (including pesticides) favour stability of farm income (Harkness et al., 2021). Income stability is, in addition to net income, an important financial indicator as it allows a better farm planning and management. Income stability in diversified and low input cropping systems is explained by, on the one hand the reduction of financial investment risks through a reduction of monetary production costs (van der Ploeg, 2021), and on the other hand a higher resilience of farm businesses to price fluctuations and extreme climatic events (Altieri et al., 2015; Lin, 2011). To be resilient (i.e. to have the capacity to absorb disturbance and still retain its basic function and structure, Walker and Salt, 2012), a system needs to include components performing the same functions but in different ways, so that the functions are maintained even if one of the components fails. It is the case in intercropping, where the (at least) two crop species grown together are (at least partly) redundant in their functions of production and income source for farmers. In the case where one crop partner fails or experiences reduced growth, the associated crop species can compensate the loss in producing higher yield than originally expected, thanks to a reduced competition for resources (or competitive release) (Döring and Elsalahy, 2022). Referred to as the insurance hypothesis (Yachi and Loreau, 1999), this compensation effect is also the basis of an increased yield stability in intercropping (Raseduzzaman and Jensen, 2017), offering a reduction of production risks over time and across environmental conditions.

Payments for environmental services are the other explanatory reason for the increased stability of income in farms investing in agricultural diversification (Harkness et al., 2021). In various countries, measures of biodiversity conservation in agricultural landscapes are supported by agri-environmental policies (e.g. in Europe, Batáry et al., 2015; in China, Zhu et al., 2018). Backed by important public subsidies (e.g. Pe'er et al., 2019), payments for environmental services aim at compensating farmers for implementation costs and potential yield losses (in the European Union at least). While monetary incentive is generally seen as key argument in most farmers' willingness to implement agri-environmental measures (Swinton et al., 2015; Zhang et al., 2015), it offers a regular and guaranteed source of income to farmers. Yet, it is worth noting that it is the agri-environmental payments, and not the direct subsidies (which largely depend on farm size in the European agricultural policy), that improve income stability, suggesting an effect of regulating ecosystem services on farm income (Harkness et al., 2021). Studies have indeed highlighted that landscape features such as hedgerows and flower or grassy strips implemented as part of subsidised agri-environmental measures to preserve biodiversity enhance the natural regulation of insect pests in adjacent crops (Sutter et al., 2018; Tschumi et al., 2016a) without significant trade-offs, such as fields becoming infested by weeds originating from the focal habitats (Cordeau et al., 2012). The enhanced regulating services provided by measures aiming at supporting biodiversity may not be seen as very surprising since biological regulation is mediated by plant and animal diversity (Dainese et al., 2019). Nonetheless, these are not trivial findings since many policy-makers (Hatt and Osawa, 2019b) and farmers (Salliou and Barnaud, 2017) do not necessarily link biodiversity conservation with regulating services useful for agricultural production.

Last but not least, agroecosystem diversification can benefit society beyond farm economies by improving environmental quality. Meta-analyses evaluating the multifunctional performances of diversified agroecosystems reveal that while favouring the natural regulation of pests, diversified cropping in general (Tamburini et al., 2020) and agroforestry especially (Beillouin et al., 2021) improves water quality and quantity. It can be explained by the positive effect of agroforestry (Torralba et al., 2016), and perennial grass strips and hedges (Vought et al., 1995), in controlling nutrient leaching and soil erosion. In addition, agroforestry, but also intercropping, can favour carbon storage in soil, potentially contributing to climate change mitigation (Beillouin et al., 2021). Finally, studies on landscape aesthetics showed that non-farmers significantly prefer diversified agroecosystems and landscapes, combining for instance trees, flower strips and a diversity of crops (Junge et al., 2011). These multiple environmental benefits of diversified cropping systems and landscapes contrast with the environmental and societal costs of pesticide use borne by society, estimated at \$9.6 billion. year^{-1} in the USA alone. This sum attributes \$1.1 billion for pesticide impact on public health, \$2.2 billion for bird losses, and \$2.0 billion for groundwater contamination (Pimentel and Burgess, 2014). While policies aiming at reducing pesticide uses has been failing at reaching their goals so far (Hossard et al., 2017), highlighting the environmental and health hazard of pesticides may convince farmers to adopt pesticide-free production programs (Finger and Möhring, 2022). Similarly, the multifunctional ecological and socio-economic performances of diversified agroecosystems, at the farm level and beyond, should be emphasized, as part of a holistic approach in pesticide-reduction policies (Möhring et al., 2020).

4. Towards an integrative framework

It is suggested that integrating the four proposed principles when designing diversified agroecosystems would create synergies favouring the control of multiple crop pests while delivering socio-economic benefits (Fig. 4). Yet, implications for scientific research and beyond towards implementing integrative diversification science are identified and discussed.

4.1. Favouring synergies to strengthen resilience

In a hypothetical diversified cropping system, one can speculate that by applying intercropping or companion planting, weeds would not affect crop yield (Verret et al., 2017), while the flowers of some of the remaining weed plants would attract natural enemies (Fig. 1). These natural enemies would have benefited from non-crop habitats at margins, such as wildflower strips composed of trait-attractive forb species. The weed plants will thus indirectly enhance biological control of insect pests (Serée et al., 2023), and complement the bottom-up effect of mixed cropping at limiting pest infestation and spread (Lopes et al., 2016). Economic benefits for farmers are expected from net yield gain (Li et al., 2020) and increased yield stability (Raseduzzaman and Jensen, 2017) offered by intercropping, pesticide reduction (Gurr et al., 2016), and potential payment for environmental services when implementing non-crop habitats (Harkness et al., 2021). Indirect benefits for society would arise from lowering the hidden costs of pesticide use (Pimentel and Burgess, 2014), improving water quality, contributing to mitigating climate change (Beillouin et al., 2021), and embellishing landscapes offering cultural services of intangible value (Junge et al., 2011).

These synergistic benefits are likely to occur over complementary short- and longer-term processes. Annual mixed crops reduce pests without delay (Zhu et al., 2000) and economic benefits from net yield gain are expected at harvest (Li et al., 2020). However, enhancing natural enemies with non-crop habitats can take 1–5 years with pluriannual wildflower and grass strips (Ganser et al., 2019), or 5–10 years with (agro)forests (Staton et al., 2019), explaining that biological control increases over the years after establishment (Thies and Tscharntke, 1999; but see Albrecht et al., 2021). Yet subsidies for semi-natural habitats are paid for at least five years and can include a bonus on year 1 to compensate the implementation costs (e.g.

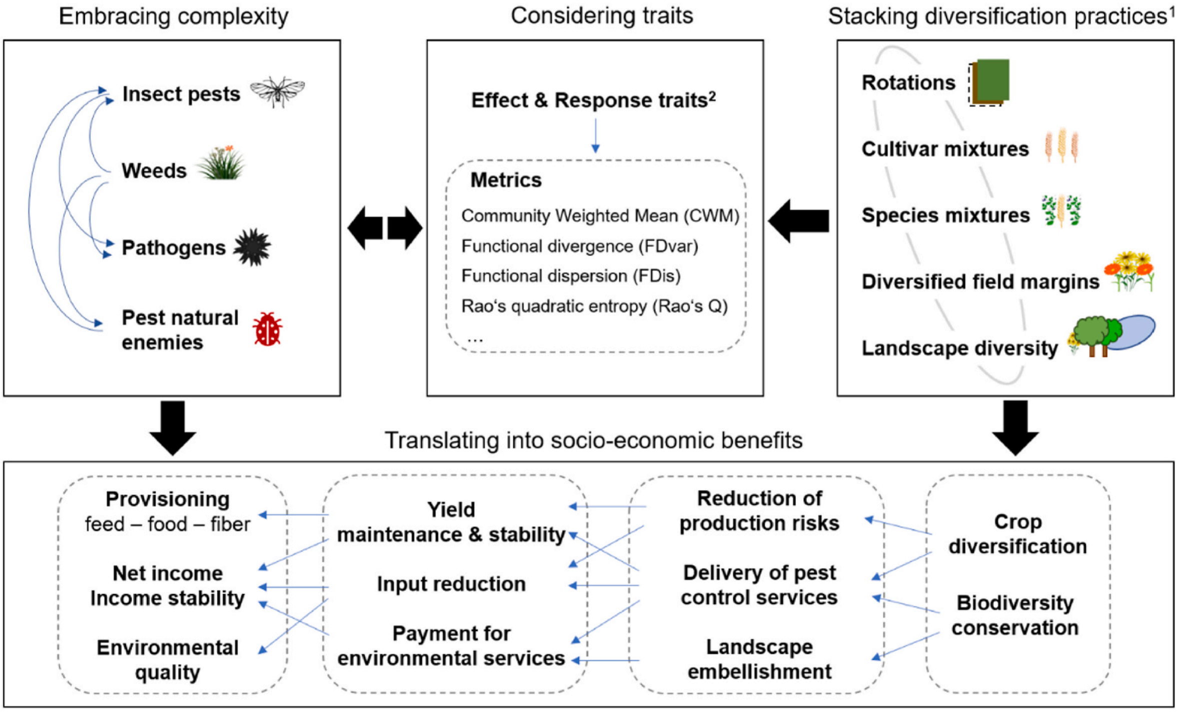

Fig. 4. Framework for an integrative diversification science to design pest suppressive agroecosystems. It invites to embrace complexity and consider the multiple pests and their enemies in interactions in highly diversified farming systems and landscapes stacking diversification practices, by considering organisms' traits through metrics capturing their mean and functional diversity effects. Resulting synergies and strengthened resilience are expected to be translated into socio-economic benefits for farmers and for the society as a whole. [1]Diversification practices are defined in Table 1. [2]A key selection of effect and response traits is provided in Fig. 2.

Landwirtschaftskammer NRW, 2022). This bonus would also compensate the delay in natural enemy enhancement and effective pest control.

This complementarity in effects is likely to increase the resilience of agroecosystems thanks to the redundancy of functions occurring at different time and spatial scales. As explained (section 3.4), a resilient system needs to include components performing the same functions but in different ways, so that the functions are maintained even if one of the components fails. When stacking diversification practices, cultural practices are based on genetic *and* species diversification while various non-crop habitats are found both at the direct field margin *and* at the broader landscape. To sustain natural enemies relying on nectar and pollen, flower resources are made available in fields (through weeds that are tolerated thanks to mixed cropping), *and* off-field with flower strips and hedgerows managed at margins. Hence, pests are controlled through top-down (by natural enemies) *and* bottom-up (through mixed cropping) effects. Finally, the stability of farms' economies is built on selling diverse commodities *and* low production costs *and* payments for environmental services. In contrast, simplified farming systems, that include a limited diversity of crops, and which base pest control on silver bullets face dramatic consequences when the unique pest control tool fails or is banned. Illustrations are the "super-weeds" (e.g. Palmer amaranth *Amaranthus palmeri* S. Wat., Amaranthaceae), which have developed in monocultures of genetically-engineered herbicide-resistant crops and become hardly manageable (Gilbert, 2013); or virus yellows transmitted by the aphid *M. persicae*, which have led to significant yield losses on sugar beet (*Beta vulgaris* L., Amaranthaceae) in Europe after the ban of neonicotinoid insecticides (Dewar and Qi, 2021).

4.2. Implications for science and research

By relying on ecological processes, any diversification approach must account for local farm context (Settele and Settle, 2018). Farming context comprises the biotic and abiotic conditions, and the management practices, at scales from the field to the landscape. It exerts a selection pressure on the assemblage of the communities, i.e. organisms, their traits, and consequently on their mutual regulation (Muneret et al., 2022). It is well acknowledged that diversification science must follow principles, rather than recipes, that must be translated locally into adaptative management practices (Duru et al., 2015). It has however several implications for scientific research.

First, it necessitates increasing the diversity of experimental environments and maximizing informational exchange. Together, this calls for collaborative—rather than competitive—research, conducted through more decentralized field trials, by multiplying autonomous experimental stations and the expansion of on-farm studies.

Second, it requires longer-term research to take into account the relentless evolutionary adaptation of farming systems (Rodrigues et al., 2022). Although crucial, long-term research is far too rare, because researchers have to deal with short-term funding and unstable positions (Butler-Rees and Robinson, 2020), and because farmer innovators have to cope with uncertain economic and regulatory perspectives (Morel et al., 2020).

Third, it demands acquiring and mobilizing broad and specialised knowledge and skills (David and Bell, 2018). It includes knowing functional biodiversity, understanding the key ecological processes at work in fields and landscapes, designing and managing complex agroecosystems, and running economically viable and socially relevant enterprises (González-Chang et al., 2020). Knowledge and skills from a variety of (sub-)disciplines are necessary. While multi- and interdisciplinarity are nowadays generally advocated in scientific research (Ledford, 2015), their realization is not trivial because each disciplinary knowledge has been specialising in an unprecedented manner, but also because each discipline has its own methods, language, frameworks, and traditions (Brown, et al., 2015).

Finally, it implies to revise and diversify the indicators of performance. Yield growth has driven the simplification of agroecosystems through input-intensive agriculture (Robinson and Sutherland, 2002), not surprisingly in an economy structured around production growth (Hickel et al., 2022). Diversification science must evaluate its performance by considering alternative indicators in addition to absolute yield. They include environmental quality comprising biological diversity and regulating processes in agroecosystems (Dainese et al., 2019), resource use efficiency (Li et al., 2020) and climate change mitigation and adaptation (Mbow et al., 2014), stability in yield (Raseduzzaman and Jensen, 2017) and income (Harkness et al., 2021). Importantly, the various indicators must be used jointly to perform integrated assessments with a view on multifunctional effects at the agroecosystem level (Boeraeve et al., 2020; Hodbod et al., 2016).

Scientific research alone, however, cannot diversify farmers' farms. Structural factors upstream and down-stream production have been identified, locking most of farms into input-intensive and simplified systems (Carlisle et al., 2022; Meynard et al., 2018). Unlocking farms and redesigning agroecosystems necessitates thinking and acting out of the box. New approaches can come from pioneer farmers whose successful radical innovations developed on the fringe of the mainstream production system radiate out to neighboring farmers and beyond, their farms becoming "agroecological lighthouses" (Nicholls and Altieri, 2018). They can also be driven by policies, with regulations and incentives exerting a significant impact on the existing system (e.g. the European Union Common Agricultural Policy represents €55 billion of subsidies annually) (Pe'er et al., 2019). Both the niche innovations and the exogenous factors (e.g. infrastructures, norms and regulations, societal concerns) impact the mainstream socio-technical system (*sensu* Geels, 2019), but they also influence each other through cross-scale feedback (a process also known as panarchy, Gunderson and Holling, 2002). Research is at the cross-road of these influences. It produces expert knowledge that must guide policy makers (Pe'er et al., 2022), it can accompany innovating farmers by objectivizing practical knowledge (MacMillan and Benton, 2014), and last but not least it teaches the current and next generations of farming and food system stakeholders (David and Bell, 2018).

5. Conclusion

Drastically reducing the use of pesticides in agriculture would require increasing plant diversity at the cropping system and landscape levels. The ecological mechanisms at play and the quantitative evidence that diversifying works in general to control the multiple pests of crops were recalled here. Yet, variability in effects and risks of failure, partially explaining the relatively low adoption of diversification practices by farmers, call for improving the science base. The present review attempted to make a contribution towards filling this gap, and proposed four principles which, adopted within an integrative framework, are expected to enhance synergies to strengthen the resilience of agroecosystems to pest pressure.

Future work will have to verify empirically the general approach proposed here. Original cropping systems and landscapes would be designed by stacking different diversification practices, where crop and non-crop mixtures would be chosen based on their beneficial effect traits. The complex interactions at play would be analyzed using the response/effect trait model, considering the diversity of interacting organisms (crop and non-crop plants, insect and micro-organism pests and natural enemies) through their functional characterization in additional to their taxonomic description. The multifunctional performances need to be quantified, allowing identifying synergies, but also potential trade-offs, in the delivery of multiple ecosystem services towards socio-economic benefits. Such empirical research should be conducted both on experimental stations and on farms, likely with iterative loops of exploration, implementation and assessments between the two.

World nations recently agreed to reduce "the overall risk from pesticides and highly hazardous chemicals by at least half" by 2030 and called to base this shift on science (UNEP, 2022). Scientific paradigms to reduce pesticides are various and sometimes propose antagonistic solutions (Altieri et al., 2017). The present review calls for an ambitious science, taking *diversity* as cornerstone, and *integration* as core strategy, to embrace the complexity of agroecosystems as multidimensional socio-ecological systems.

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Data availability

No data was used for the research described in the article.

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