CHAPTER FOUR

Promoting crop pest control by plant diversification in agricultural landscapes: A conceptual framework for analysing feedback loops between agro-ecological and socio-economic effects

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Contents

Abstract

Given the negative environmental effects of conventional agricultural techniques, the need for biodiversity-friendly agriculture systems that rely more on ecosystem services and less on chemical inputs is becoming increasingly urgent. In this paper, we focus on crop protection strategies that are alternatives to the use of pesticides. Diversification of the plant component of agricultural areas at different space and time scales has been presented as a powerful socio-economic and agro-ecological mechanism for the sustainable control of pests. Our interdisciplinary group of scientific experts examined the literature on the ecological effects of plant diversification on pests and their natural enemies, as well as the social science literature on the conditions for farmers to adopt the corresponding practices, to assess the potential offered by plant diversification.

We developed a conceptual framework that connects the agro-ecological and socio-economic components of an agricultural landscape in a dynamic loop accounting for interactions among elements at different spatial and temporal scales and their feedback effects. This article presents this framework and illustrates its application to the case of wheat production and protection. By explicitly connecting each level of agro-ecological organization with the potential socio-economic drivers and limitations underpinning the adoption and implementation of plant diversification in landscapes, this framework makes it possible to analyse the synergies and antagonisms between different modes of diversification and the conditions of their deployment. Exploring this framework is a prerequisite to the identification of opportunities and key feed-back loops for designing diversification strategies that unlock the agro-ecological potential of future production systems. We conclude that there is a need for interdisciplinary research in experimental landscapes involving farmers and other local stakeholders to design sustainable future agricultural landscapes that deliver high levels of biological control services.

1. Introduction

The spatio-temporal diversification of both non-cultivated and cultivated plants in agricultural landscapes is recognized as a central pillar of agro-ecology (Altieri et al., 2009; Duru et al., 2015a; Lechenet et al., 2016; Malezieux et al., 2009), which can be exploited to enhance the multifunctionality of agroecosystems (Dore et al., 2011; Kremen et al., 2012; Tamburini et al., 2020). Plant diversification includes, for instance, mixes of different crops and their cultivars, agroforestry, diversified crop rotations and agro-ecological infrastructures.

By combining crops and non-cultivated plants at all relevant spatio-temporal scales, diversification promotes multiple species associated with wildlife-friendly agriculture and enhances the provision of various ecosystem services to agriculture (Grass et al., 2021). Reviews of the ecological literature attest to the overall positive effects of plant diversification on the regulation of pests including pathogens, herbivores and weeds (Barbosa et al., 2009; Civitello et al., 2015; Tamburini et al., 2020). Yet, the mechanisms that underlie such effects, such as barrier, dilution and complementary resources, depend on the biology of the pests and their enemies and are influenced by multiple biotic and abiotic variables including landscape heterogeneity (defined by its two components, composition and configuration of crop and non-crop habitat patches) or pedoclimatic conditions (Fahrig et al., 2011). This variation in biological response may explain the inconsistency of pest and natural enemy responses to landscape heterogeneity and, in several cases, the low efficacy and adoption of diversification practices by farmers derived from promising concepts (Chaplin-Kramer et al., 2011; Karp et al., 2018).

From the agronomic perspective, existing strategies for the diversification of vegetation and for crop protection are intimately linked (Altieri, 1999). Field-level crop rotations have been used as a method of controlling pests and diseases for at least 6000 years, and during the 18th and 19th centuries revolutionized crop productivity. With the development of synthetic chemical pesticides, however, farmers in industrialized countries have simplified crop rotations, often toward highly profitable cash crops, and farms have become increasingly specialized since the latter half of the 20th century. This evolution has strongly influenced and simplified landscape composition. The adoption of cash crops and their associated intensive production practices has come with a series of technological changes and agricultural systems exhibit locked-in and inflexible behaviours (Meynard et al., 2017). These systems have evolved for decades in a self-reinforcing way due to the dependency to agrochemical inputs (Carpentier et al., 2005; Milgrom and Roberts, 1995). This increasing reliance on technological solutions to control pest and secure production has rendered less visible the intricate socio-ecological interactions that previously underpinned agriculture and the provision of ecological services, such as pest regulation. Designing cropping systems that are mainly based on the functioning of ecosystems will therefore require a breakage of this self-reinforcing, locked-in socio-technical and economic cycle, jointly in farming systems, agricultural value chains[a] and natural resource management domains (Duru et al., 2015b). It requires the development of coupled-innovation, both along the value chain (Meynard et al., 2017) and at regional levels for the organization and design of landscapes.

The effects of plant diversification on pest regulation are intrinsically linked to the spatio-temporal scales considered (Ratnadass et al., 2012). This makes the mismatch between ecological processes (from organisms to biogeographic area) and agricultural-sector management (from seed to food and feed distribution) an obstacle to the integration of disciplinary knowledge (Pelosi et al., 2010). Improving pest regulation would require specific management responses to influence ecological processes at every scale. Systematic integration of this knowledge will then be necessary to guide the design of sustainable, future agricultural landscapes (Duru et al., 2015b).

In facing this issue, the French ministries for Agriculture, for the Environment and for Research (MAA, MESRI, MTES) asked the French National Research Institute for Agriculture, Food and the Environment (INRAE) to carry out a collective scientific assessment (INRA-DEPE, 2018; Pesce et al., 2021), on the use of plant cover diversification at several spatial and temporal scales to protect crops. A multidisciplinary committee of around thirty scientific experts was established in 2020 to inventory the international, peer-reviewed literature. The assessment aims to evaluate the

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[a] A value chain in agriculture identifies the set of actors and activities that bring a basic agricultural product from production in the field to final consumption, where at each stage value is added to the product.

potential of the management of plant diversity as an agronomic opportunity to regulate pests and reduce the use of chemical pesticides, the socio-economic conditions for the deployment of such crop protection strategies, and the effects of their implementation on the supply of other ecosystem services and biodiversity. This article presents the conceptual framework adopted by the committee as a prerequisite to carry out the literature review.

Recent conceptual frameworks to analyse the issues of an agro-ecological transition to sustainable landscapes have relied on the socio-ecological system concept (Ostrom, 2009). Socio-ecosystems are complex systems composed of many interacting social, economic, political and ecological elements, organized in different nested levels (Ostrom, 2009). Socio-technical systems are a sub-element of a socio-ecosystem, and this terminology refers to the co-evolution of social and technical aspects of the socio-ecosystem, such as changes that might occur in the wheat transformation sector (Savaget and Acero, 2018). Lescourret et al. (2015) and Gerits et al. (2021) highlighted that an explicit consideration of both ecological and socio-economic dynamics are crucial for the design multi-functional agricultural landscapes. However, the framework of Lescourret et al. (2015) does not sufficiently consider the multiple spatio-temporal scales involved (for example, the international scale associated to seed sectors, or the long term associated to evolutionary processes), while that of Gerits et al. (2021) does not account for the agronomic components of the system, which may seem surprising for a study on agroecosystems. Duru et al. (2015b) integrated the farming system[b] and socio-technical system into their socio-ecological approach to develop an integrated framework highlighting the need to consider, simultaneously, the functioning of farms, agricultural value chains and natural resource management for agro-ecological system design at local level. However, the ecological dynamics of pests that occurs at the different spatio-temporal scales are rarely considered. It is necessary to address the complexities of the provision of the service of pest control, by considering the feedback loops that connect the social and the ecological components of the agricultural system though farming practices.

In this article, we extend the interdisciplinary framework of Vialatte et al. (2019), which aimed to facilitate the study and governance of multiple

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[b] The farming system is a population of individual farm systems that have broadly similar resource bases, enterprise patterns, household livelihoods and constraints, and for which similar development strategies and interventions would be appropriate, Dixon et al. (2001).

ecosystem services in agricultural social-ecological landscapes. Our extension combines socio-economic, ecological, and agronomic components of agricultural systems in a conceptual framework that provides a dynamic, theoretical basis for analysing the effects of plant diversification on pest control. It proposes a holistic view of these nested components, which scales from organisms to the biogeographic area and from crop varieties to agricultural value chains, and to the design of governance of agroecosystems, considering both services and disservices in agricultural landscapes. This framework makes explicit the disciplinary knowledge required to investigate the effects, drivers and limitations of plant diversification for sustainable crop protection.

The conceptual framework presents three key components, each of which is specified according to the major levels involved in crop protection and should be considered for the governance of agricultural landscapes:

(i) The agro-ecological compartment organized at different levels, from an organism to the biogeographic area.

(ii) The socio-economic compartment also organized at various levels, from crop varieties to territory. A territory is a socio-economic landscape and can be defined both as the spatial extent across which stakeholder networks are built, maintained and interact, influencing farming practices (Caron, 2005). The social compartment also includes all institutions that influence social and socio-ecological interactions, often extending beyond the boundaries of the territory.

(iii) The agricultural landscape resulting from land use and farming practices. It is the point of intersection of the two agro-ecological and socio-economical compartments. It can be viewed as a dynamic mosaic of habitat patches made of cultivated fields, devoted to agricultural production, and less- or non-productive, semi-natural habitats.

The effects, drivers, and limitations of plant diversification for pest control are examined in 11 steps, set within a dynamic loop, whose central point corresponds to the agricultural landscape and the interconnected agro-ecological and social compartments. In this paper, we outline the main effects of plant diversification at different spatio-temporal scales on pest regulation described in the literature (steps 1 to 6). The potential agronomic, socio-economic, and ecological impacts of deploying plant diversification at the landscape level as reported in the literature are then highlighted. Finally, we draw up the opportunities and constraints for the deployment of different modes of diversification in the production sector (up- and down-stream) and in institutions, and discuss how to facilitate deployment as part of future agricultural landscape management (steps 7 to 11).

This approach is explored using wheat as an example, case study production system. This choice is motivated by:

(i) the importance of this crop in temperate agricultural production systems (e.g. Martin et al., 2021);

(ii) the number and diversity of wheat pests in the world (weeds, pathogens, insects) and their associated losses (overall wheat losses by pests estimated at 28% (Oerke, 2006));

(iii) the abundance of the literature for this crop, which has supported numerous meta-analyses and reviews;

(iv) the current socio-economic organization of the wheat commodity sector, which determines the agro-ecological innovations that can be adopted.

2. Conceptual framework and application to wheat systems

Fig. 1 illustrates the conceptual framework. We go over the 11 steps (① to ⑪) of plant diversification's social-ecological effects, drivers and limitations.

① The agricultural landscape is the central level of organization of the framework, bringing together the various levels of agro-ecological and social components that are involved in plant diversification. The landscape is composed of patches of crop fields and semi-natural habitats, themselves composed of different cultivated or non-cultivated plants. Some elements that make up the landscape belong to both the agro-ecological and social components. This is the case, for example, of certain phytophagous species, which belong to the local species pool, and which are qualified as pests.

At the plant level (1a), diversification concerns the genetics of plants and their phenotypes and traits (e.g. phenology, morphology, immunity or resistance, nutritional status), which in turn can affect interactions with other species. In particular, it corresponds to varieties for crops, with related pests and natural enemies.

Plant diversification can be achieved within the field, spatially or temporally, by intra- or inter-specific plant associations (e.g. varietal mixture, intercropping, beetle banks) and diversified rotation (temporal diversity) or through semi-natural habitats in field edges and margins (1b). At this level, the dynamics of pest populations in diversified plant communities result from both multitrophic interactions (e.g. predator-prey) and selection by local agricultural practices (diversified cover, tillage, use of pesticides, fertilization, etc.).

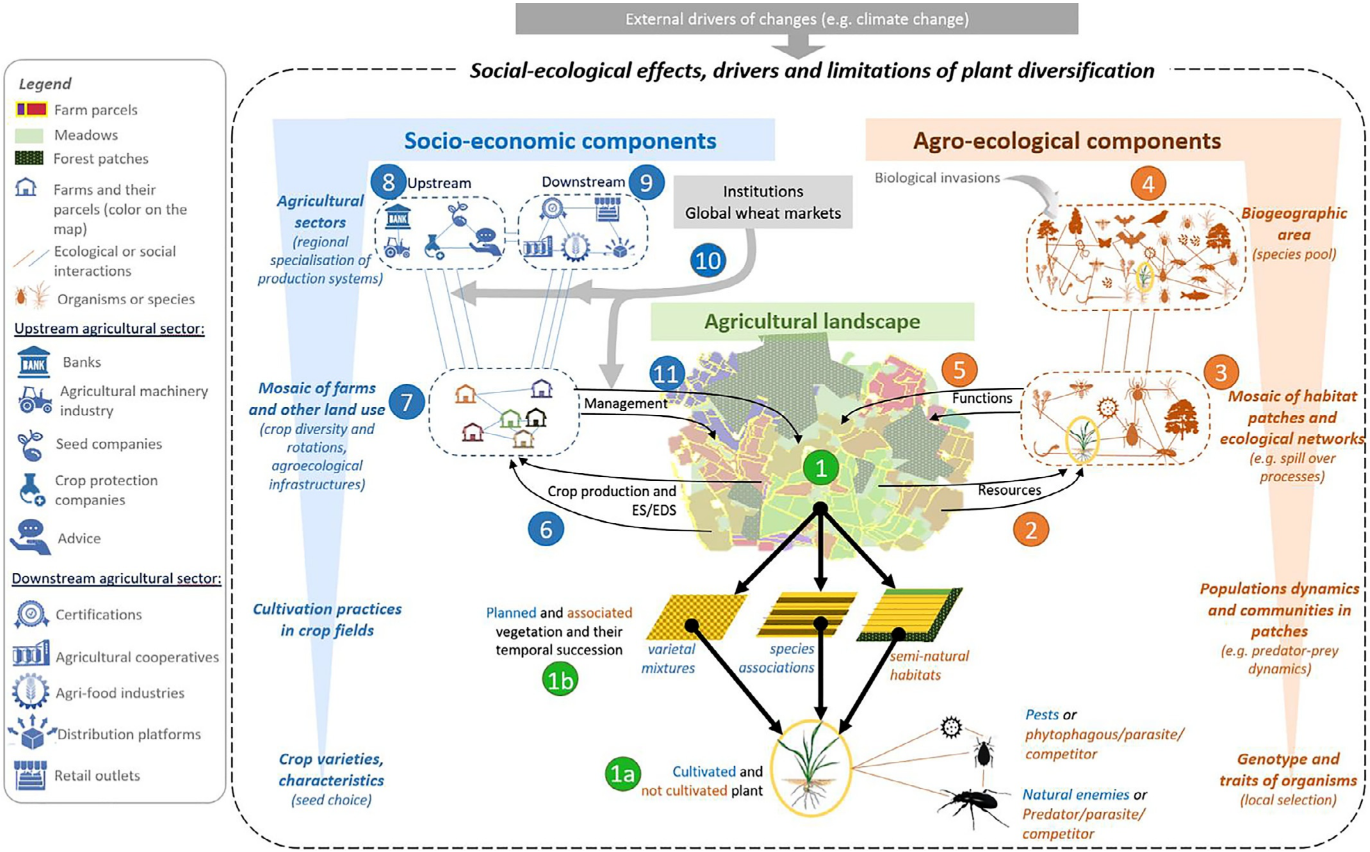

Fig. 1 See figure legend on opposite page.

Notably in wheat, many of the different modes of plant diversification have been found to have positive effects on the control of a variety of pest groups:

Within-field, intra-specific crop diversity

Meta-analysis has shown that variable efficacy of intra-specific crop diversification, predominantly depends on pest pressure, often induced by climatic conditions (Dubs et al., 2018). The efficacy of varietal mixtures is particularly noticeable for fungal wheat pathogens causing aerial diseases (e.g. stripe rust and septoria tritici blotch) rather than those causing soilborne diseases (Hariri et al., 2001; Kristoffersen et al., 2020; Saur and Mille, 1997). Effects are stronger in low input cropping systems as highlighted in trials where crops were not treated with synthetic fungicides (Borg et al., 2018; Reiss and Drinkwater, 2018). A higher abundance in spiders and springtails in crop varietal mixtures illustrates the complexity of effects due to trophic interactions (Chateil et al., 2013), while weed control appears to be limited by intra-specific crop diversification (Lazzaro et al., 2018).

Within-field, inter-specific crop diversity (intercropping)

Inter-specific diversification by increasing plant species diversity within the field promotes predation and parasitism (Wan et al., 2020), and different plant species may be cultivated with wheat (primary crop) to enhance pest control. Wheat-clover intercropping helps managing weeds during the wheat cultivation and post-harvest due to the clover residues mulching the soil (Vrignon-Brenas et al., 2018). Overall, intercropping has been found to provide weed and disease control, with the evidence for insect control being weaker (Stomph et al., 2020). When wheat is sown as an intercrop

Fig. 1 Conceptual framework for analysing social and agro-ecological effects, drivers and limitations (with feedback loops) of plant diversification in agricultural landscapes. The 11 steps are summarized in three main components: (i) the agro-ecological compartment organized at different levels (from organisms to the biogeographic area, in orange); (ii) the socio-economic compartment also organized at various levels (from crop varieties to organization of the agricultural sectors at the territory, in blue), with the institutions (often going beyond the boundaries of the territory) that influence social and socio-ecological interactions (in grey); and, (iii) the agricultural landscape resulting from land use and practices (in green). *Adapted from Vialatte, A., Barnaud, C., Blanco, J., Ouin, A., Choisis, J. P., Andrieu, E., et al. 2019. A conceptual framework for the governance of multiple ecosystem services in agricultural landscapes. Landsc. Ecol. 34 (7), 1653–1673. doi:10.1007/s10980-019-00829-4.*

in potato or musk melon, and not as the primary crop, it has been found to provide an effective barrier against aphid pests (Hooks and Fereres, 2006).

Temporal diversity of cultivated and non-cultivated plants (rotation)

The temporal diversity of plant cover, at the field scale, is primarily driven by farmer decision-making for crop rotations, cover cropping and green manures. Rotations have been used to reduce plant diseases, weeds and pests (McLaughlin and Mineau, 1995). For instance, *Brassica* crops have proven useful in wheat rotations because of their biofumigation properties, which help to control soilborne wheat diseases like *Rhizoctonia* sp. (Larkin, 2015). Diversifying rotations reduces weed densities (by 49% compared to a basic rotation with one or two crops) and this reduction is primarily due to sowing date variation rather than crop diversity (Weisberger et al., 2019). When looking at the seedbank, a hierarchy of effects from sowing date, crop type and herbicide is found (Bohan et al., 2011). Regardless of the environmental context and herbicide use, the effect of rotation diversification on weeds is stronger under no-till than under tillage (Weisberger et al., 2019).

The plant diversity of field edges

Field edges and margins (grassy strips, flower strips, hedges) can be a source of natural enemy populations, such as aphid parasitoids and carabids in wheat fields (French and Elliot, 2001; Zumoffen et al., 2018). However, the spill over of natural enemies from the field edges into the core of wheat fields appears limited for other taxa, such as spiders (Armendano and Gonzalez, 2010; Seyfulina, 2010). Non-cultivated Poaceae at the edge of the field do not appear to be a source of aphids colonizing the adjacent wheat (Vialatte et al., 2005). Moreover, some grasses and other specific plants should be considered as a disservice, as they can be a source of pathogen inoculum (*Fusarium* sp., *Ustilago* sp., *Tilletia* sp., *Claviceps* sp.; e.g. Mourelos et al., 2014) and alternate disease hosts (*Berberis* sp. for the rust pathogen *Puccinia graminis* f. sp. *tritici*; Burdon and Thrall, 2008, Zhao et al., 2016).

Large-scale adoption of each of these modes of diversification could have marked ecological and agronomic repercussions if adopted the landscape scale. The widespread use of the common mixture of wheat cultivars would increase the risk of multivirulent selection, depending on the biology of the pathogen (Mundt, 2002; Papaix et al., 2011; Phan et al., 2020; de Vallavieille-Pope et al., 2012). Moreover, the increase of within-field diversity might eventually lead to a trade-off with varietal diversity at the landscape scale. The deployment of numerous agro-ecological infrastructures such as edges and margins adjoining to the fields would promote beneficial organisms, but can also inadvertently support disservices (e.g. inoculum sources). The large-scale adoption of plant diversification methods therefore requires landscape-level coordination between all stakeholders to optimize the balance of positive and negative outcomes.

② At the landscape level, plant diversification concerns the landscape mosaic which, from an agro-ecological point of view, provides resources for species (including pests and natural enemies) over their life cycle (e.g. refuge, food, and reproduction sites). Resource availability depends on the spatial and temporal composition and configuration of habitat patches (landscape heterogeneity) that is determined by human decision-making.

③ Cultivated fields and semi-natural habitats are connected in time and space by the dispersal of organisms, giving rise to complex interaction networks. Importantly, pest control services in the cultivated fields depend on the surrounding landscape of cropped and non-cropped habitats.

High landscape heterogeneity benefits natural enemy populations and communities, although its impact on pests and pest control remains unclear (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Karp et al., 2018; Veres et al., 2013). Semi-natural habitats and cultivated fields provide complementary food resources or overwintering sites for natural enemies (e.g. hoverflies: Vialatte et al., 2017, Raymond et al., 2014), but the relative importance of these structures, their interaction with human decision-making and their effect on pest control are difficult to disentangle and remain unclear (Petit et al., 2020). In wheat fields, local agricultural practices (e.g. pesticide use, tillage frequency/depth, number of varieties) appear to have a stronger impact on richness and abundance of natural enemy communities than the landscape structure surrounding the fields (Puech et al., 2014). Weed communities, on the other hand, appear to respond to the effects of landscape structure rather than to the local intensity of practices (Alignier et al., 2017).

The main source of aphids colonizing wheat fields in autumn is found to be maize (Gilabert et al., 2017; Vialatte et al., 2006), which is a sink of virus populations (BYDV) transmitted by *Rhopalosiphum padi*. Aphid and hoverfly abundances in wheat fields in early spring are positively associated to the forest area in the surrounding landscape, while aphid parasitism is higher near hedges in late spring (Alignier et al., 2014). Grassland meadows are a reservoir of natural enemies (Schneider et al., 2013). Hedges also favour carabid dispersal, as many carabid species overwinter in forest edges and spill over onto the wheat fields in spring (Roume et al., 2011). The proportion of oilseed rape present in the previous year favours carabid abundance in wheat fields (source effect), while the occurrence of rapeseed in adjacent fields in the current year decreases carabid abundance in the wheat (Marrec et al., 2017).

Although the complementarity between different types of semi-natural environments in terms of pest control potential remains poorly studied, and appears to be taxon-dependent (Badenhausser et al., 2020), the literature seems to converge to a figure of about 20% of the surface area being assigned to semi-natural habitats in agricultural landscapes for the support of natural enemies (Gagic et al., 2021; Martin et al., 2019; Tscharntke et al., 2021). For the crop mosaic, increases in crop diversity and decreases in field size have been found to be positive factors for biodiversity and biological control in agricultural landscapes (including wheat, Redlich et al., 2018, Sirami et al., 2019). The proportion of semi-natural habitats, field size and crop diversity in the landscape jointly drive the potential associated diversity that can occur in the different fields (Gagic et al., 2021; Martin et al., 2019; Tscharntke et al., 2021). With large-scale dispersal of organisms between habitats, coordination of crop rotations at the landscape scale might be used to favour natural enemies while reducing pests by promoting or limiting certain combinations of crops within and between years.

④ The presence in the landscape of species from the regional (biogeographic area) pool depends notably on local resources and human practices, which act as filters. Regional climatic conditions and their changes also influence ecological networks.

Processes at the landscape level, such as spill over, interact with the processes at the regional level (e.g. migration) to explain the aphid-parasitoids trophic interactions networks and the provision of biological control services in cereal fields (Andrade et al., 2015). However, the parasitoids of wheat aphids appear to be more sensitive to vegetation diversification at farm level than at regional level (Brewer et al., 2008). More generally, regional climate and habitat connectivity are among the main risk factors for pest invasion in agricultural areas (Fears et al., 2014).

The risk of pest emergence is expected to increase with climate change. In the UK, wheat is likely to develop earlier in the season, favouring infection with Fusarium ear blight (Madgwick et al., 2011). The diversification of landscapes, to promote the resilience of biological control in the face of climatic events, may be effective in limiting the risks of emergence and outbreaks linked to climate change (Feit et al., 2021). Managing habitat connectivity at large scales requires assessing the cost-benefit balance: while it increases invasion risk, it also promotes movement of natural enemies (Tscharntke et al., 2015).

⑤ Different species perform ecological functions that ensure the ecosystem functioning, such as primary production and natural regulation.

⑥ Ecological functions underpin ecosystem services, such as pest control, and disservices, including pest outbreaks, from which the social part of the landscape experiences costs or reaps benefits. These include increases or decreases in the use of synthetic pesticides to control pests, as just one example. Farmers have to face agronomic damage, caused by crop yield and/or quality loss.

Here, we focus on the agronomic literature that has explicitly quantified pest control and/or its benefits, including the incidence of disease, predation rate, pest damage and yield loss and not only the relative pest and/or natural enemy abundances more usually considered in the ecological literature.

Beillouin et al. (2020) conducted a meta-analysis of a wide range of diversification strategies at the crop-field scale. This showed that plant diversification can boost pest control by 63%, decreasing damage and enhancing crop yields by 13% on average. Varietal mixtures may also maintain high yield potential, while reducing herbicide treatments by half (Oveisi et al., 2021). Plant intraspecific diversification has a generally positive effect on yield in wheat fields (+3% of yield on average, but with a large variation), and reduces interannual yield variability (Borg et al., 2018; Kiaer et al., 2009; Reiss and Drinkwater, 2018). Cereal-legume intercrops reduce disease damage by 33% (Zhang et al., 2019) and improve yields and stability (Bedoussac et al., 2015; Raseduzzaman and Jensen, 2017).

Perennial, species-rich flower strips can significantly reduce the number of cereal leaf beetles while also increasing the yield of nearby winter wheat by 10% (Tschumi et al., 2016).

At the landscape scale, a quantitative synthesis across multiple crops (including wheat) showed that pest control by natural enemies in crop fields was 1.4 times higher in landscapes with low proportion of arable land and high edge density than in landscapes with low edge density (Martin et al., 2019). Another quantitative synthesis showed that landscape simplification and the loss of semi-natural habitats would reduce biological control by 46% (Rusch et al., 2016). Biological control in wheat fields with high landscape-level crop diversity appears 8 to 33% higher when compared to low diversity landscapes (Redlich et al., 2018).

These results suggest at a considerable potential for the use of functional diversity for pest management. However, to translate improved pest management into increased yield, which is a composite variable resulting from multiple direct and indirect agronomic, soil, climatic and ecological factors, agricultural practices must be explicitly considered in their landscape context (Ricci et al., 2019, but see Puech et al., 2015).

⑦ Farmers are dependent for certain ecosystem services and disservices, including pest control on ecological networks that result from the structure of and management practices in the landscape.

The most promising modes of diversification of plants, in terms of efficiency and acceptance among agricultural stakeholders, appear to be by modification of the within field lay out, such as the installation of grassy strips within fields. Diversification of plants at the landscape scale appears as more difficult to implement (Salliou et al., 2019). Pest control is largely done via an individual decision-making process managed by each farmer, individually. This individual freedom of action may be modulated in interaction with supply chains and technical advisors (Barnaud et al., 2018). Farmers are thus more likely to embrace within-field management approaches than collective management practices. Pests and their natural enemies, together with the landscape structure, represent common goods in the sense described by Ostrom (1990). Their management requires coordination at the landscape scale, which has little chance of spontaneously emerging from unregulated interactions between individual farmers (Cieslik et al., 2021; Costello et al., 2017). Such collective management requires polycentric governance mechanisms (Biggs et al., 2012; Ostrom, 2010), which may be hampered by strategic interactions which can lead to free-riding, i.e., strategically letting the other farmers enhance biological control in the landscape (Wilen, 2007). One example of polycentric governance is the development of economic and environmental interest groups, such as the GIEE (2021) in France who deal with specific local agro-ecological issues. Farmers, on the other hand, see the landscape as a resource for pests rather than a source of biological pest control (Salliou and Barnaud, 2017). Diversifying the landscape by planting hedges, for example might generate issues at the farm level because some of the related benefits would be shared with other farmers in the landscape, while the cost in terms of lost producing area remains individual (Atallah et al., 2018; Fenichel et al., 2014; Miranowski and Carlson, 1986). Scientific uncertainties about the efficiency of such practices, the availability of management practices and tools that reduce risk (e.g. pesticides) and the possibility of losing individual decision-making autonomy are all identified as key factors determining the current individual and collective farmer strategies (Duru et al., 2015a,b; Salliou et al., 2019; Salliou and Barnaud, 2017).

⑧ The possibilities for farmers to diversify the plant component of their fields depends on constraints along the agricultural value chain, in particular regarding the availability of seeds, technical support and tools upstream in the value chain.

⑨ Other constraints associated to downstream are imposed on farmer decision-making, such as through agricultural product standards and economic opportunities.

After the second world war, cash crop specialization allowed farmers to develop agronomic practices and knowledge on a limited number of crops (e.g. Zentner et al., 2002), resulting in marked increases in the relative share of those crop by acreage. The development of specialized farms led to the emergence of services upstream in the value chain, for providing agronomic advice, seeds and chemical inputs. The value chain became more and more integrated, with firms supplying these inputs to farmers and also buying their production, thereby influencing modes of production via contracts, production guidelines and quality standards. Alongside this specialization of farms, large specialized production regions emerged, resulting in reductions in logistic costs at harvest and critical market size for export infrastructures, such as cooperatives in France (Filippi and Triboulet, 2011). Such a system has evolved for decades in a consistent, self-reinforcing way (Carpentier et al., 2005; Milgrom and Roberts, 1995). It was supported by increasing investment in Research and Development for the main cash crops, such as the huge market for wheat, and a reduced research effort on minor crops with much smaller markets (Meynard, 2013).

Currently, diversifying rotations on farms leads to three main types of constraints, including: higher workloads; limited outlets for unconventional crops introduced into rotations; and, short-term economic impacts due to the reductions in the production of cash crops such as wheat. Land-use decisions for cropland take into account business prospects, which depend on the quantity and quality produced. Management of mixed harvested products, such as would happen with intercrops, may also be considered as a limit for accessing markets which demand vast, homogeneous and constant supplies of agricultural products. In many cases, the access to market of agricultural production is realized by intermediates collecting from farmers and selling on markets large quantities of agricultural commodities. These intermediates are able to manage the supply and reduce price volatility by storing excess production (Hannachi, 2011). Imposed restrictions on homogeneity of quality, for example, are required by transformation agro-food firms as a condition of marketability (Le Bail and Valceschini, 2004). Wheat production is particularly constrained by product uniformity requirements. Millers keep homogeneous batches of each variety in order to make their own flour blends based on recipes that they sell to food processing companies that specialize in bread, cookie and pasta manufacture. These patterns in the value chain restrain the capacity to develop resistant cultivars and generalize their use at large scale (Lamine et al., 2010).

Combinations of intercropped species, such as wheat sown with peas, may necessitate grain sorting following harvest. Farmers, who must purchase specialized equipment, are typically left to handle this responsibility by cooperatives (Magrini et al., 2016). A group purchase of this type of equipment would be a good approach to limit equipment costs, and might encourage landscape scale cooperation among farmers.

The use of labels (certification) can act as an opportunity or as a constraint for farmers to adopt plant diversification, depending on the ambitions of the certification body for the diversification. Being certified Organic, which prohibits the use of synthetic pesticides, may indirectly lead to a diversification of plant cover to promote natural regulation as an alternative to pesticide use. However, plant diversification issues are not intrinsically linked to organic farming in field crop systems such as wheat, and diversification measures can be deployed in conventional systems (Tscharntke et al., 2021). High environmental value (HEV) certification, on the other hand, requires a minimum proportion of semi-natural elements, which has already been reached in the vast majority of French farms, thus limiting any further increase in diversification for some certified farmers.

⑩ Institutions influence social and socio-ecological interactions through, for example, public incentives, regulatory policies and the development of scientific knowledge.

Recent trends in institutional and public policies favour diversification of plants to support a number of ecosystem services. Longer and diversified rotations are encouraged via green payment incentives as part of the first pillar of the CAP or as part of the Agri-Environmental Climate Schemes (AECS) proposed in the second pillar. Subsidies are also used to maintain pasture land, semi-natural habitat elements and to support agroforestry (Lefebvre et al., 2012). Such payments can act as drivers of diversification, to which some farmers respond, but can also represent barrier to diversification. Where the minimum eligible rotations supported by payments have low diversity, for example, these may be selected and payments may lead either to no change or even lower crop diversity. Indeed, the 2014 greening of the CAP measure which supported diversified rotations have had a very minor effect on land allocation (Louhichi et al., 2018), affecting only 4.5% of the agricultural landscapes in Europe. This limited effect has been documented (Gocht et al., 2017; Mahy et al., 2015; Schulz et al., 2014) and explained by the low ambition of the policies in terms of diversification (Pe'er et al., 2019), the definition of so many exceptions that 45% of farms and 14% of the area were not covered by the regulation constraints, as well as a too broad definition of "Ecological Focus Areas". Regarding wheat production, the AECS "crop system" is associated with a requirement to diversify crop cover, with a target of 5 different crops over a 5-year period, but this incentive program is voluntary. Future sustainable agricultural landscapes will therefore requires that public policies are appropriately constructed, fostering an agro-ecological transition to sustainability.

Regulations on seed quality impose strong constraints on farmers through the DUS (Distinction, Uniformity, Stability) requirement for variety registration, as a tool to assure plant breeder property rights. Conventional breeding, which produces genetically homogeneous varieties such as pure lines for wheat, is designed for that purpose, and has resulted in a standardization of vegetal genetic material (Hermesse et al., 2018). Intellectual property rights for new wheat varieties further increases the constraints on the seed sector and results in little diversification (Grimonprez, 2012, 2017; Hermitte, 1990). Alternative breeding methods, such as on farm selection, participatory plant breeding and reintroduction of ancient landraces generate more diverse varieties but do not readily fit into the regulatory system. New legislation and regulation to allow selection by farmers of varieties adapted to their local environment and practices would be an important step toward sustainable future agriculture landscapes (van Frank et al., 2020).

Research and Development also generate constraints and opportunities by offering new diversification options to farmers. R&D is more dynamic in large markets, such as the wheat market, than for diversification crops

(Charlot et al., 2015). As such, it will be easier in the short-run to diversify production within field than in rotations. A possibility is to (study and) use mixes of registered varieties, as currently experienced in France and Denmark (Labarthe et al., 2021).

⑪ Plant diversification practices can be adopted in response to current agricultural policies, prices, standards and advice, and where farmers in their own observe sufficient levels of pest control and neighbouring fields.

While the literature testifies to a general, positive effect of plant diversification practices on pest control, it also emphasizes the context-dependence of the observed effects. As plant diversification practices have different management time-scales, some flexibility and adaptation is needed for appropriate local deployment, depending upon the biophysical, meteorological, and socio-economic context. Crop varietal mixtures make it possible to assemble different, complimentary combinations of resistance traits to pests and diseases at a local level, with great flexibility. Grass and flower strips persist for a number of years, but can also readily be created and modified to produce specific patterns (Ernoult et al., 2013). Hedgerows and agroforestry require more time to produce a valuable effect, with the full agro-ecological benefits only manifesting a few years, decades or even centuries after adoption (e.g. Alignier et al., 2020).

Plant diversification practices directly affect the landscape structure ①, and then via the available resources for organisms involved in natural regulation ②, pest control. The conceptual framework we describe here is therefore intrinsically dynamic.

3. Discussion and Conclusion

An analytical framework allowing an interdisciplinary analysis of crop protection strategies relying on plant diversification (Fig. 1).The framework explicitly attempts to represent the range of organization levels and of associated potential socio-ecological opportunities and constraints underpinning plant diversification in the context of an agro-ecological transition to sustainable pest control. The goal is to eliminate any potential ambiguity across scientific disciplines, allowing an interdisciplinary approach to future plant diversification. It may also serve as a medium for communicating the multi-scale complexity and linkages between the ecological and social functioning of agricultural socio-ecosystems. Each mode of plant diversification and its spatial and temporal effects can be precisely positioned in the framework. These properties are important for highlighting the agro-ecological basis of diversification modes and their performance and the current socio-economical limitations of their implementation at the field, farm and landscape scales. This is a prerequisite for designing how to combine these drivers and to identify key feed-back loops to account for when designing diversification strategies in order to unlock the current production systems.

Positive ecological effects of plant diversification on wheat pest regulation, but knowledge gaps for the links between pest regulation level, crop damage and yield.The effects of different modes of plant diversification, across spatial and temporal scales, tend to be most often positive for the regulation of wheat pests. Yet those effects are overall highly variable from one social-ecological context to the other. Thus, a scientific challenge lies in achieving a more thorough understanding of this variability and the key drivers to promote effective diversification strategies. A key gap in scientific knowledge, and a barrier to the adoption of strategies of diversification by farmers and their advisors, is linked to the fact that the long-term impacts of pest control (and other ecosystem services) and its consequences on yields are uncertain and context-dependant (Duru et al., 2015a; Salliou and Barnaud, 2017). While many scientific studies deal with ecological issues, few of them handle impacts of pests on crop production or damage, strongly limiting the utility of the available scientific literature for agricultural stakeholders (Petit et al., 2020). It is possible that combining plant diversification modes will reduce uncertainty and risk in pest control, but it may also come at the cost of undesirable socio-ecological interactions. There is currently too few field-research that has looked at diversification modes in combination, notably combining actions at plant, field and landscape levels (Petit et al., 2020). Developing agro-ecology at field, farm and landscape levels requires deciphering the multiple ecological interactions underpinning the emergence of pest control services (Jeanneret et al., 2021). Modelling approaches have attempted to explore these interactions, but have done so only incompletely. *Landsepi* (Rimbaud et al., 2018) explicitly works at different spatial scales to simulate the cropped landscape epidemiology and evolution of plant diseases, but does not consider the role of the semi-natural elements. Non-cultivated plants appear to play a central roles for the provision of ecosystem services such as pollination (Bretagnolle and Gaba, 2015) and biological control (e.g. Madden et al., 2021), particularly within fields.

Current socio-technical limitations and constraints for the implementation of crop diversification at large scale and the interest of collective action to overcome them.

Several constraints were identified at the upstream and downstream value chain levels, related to logistics (inputs, crop productions), farmer knowledge (individual skills, R&D organization and dissemination of knowledge), and economic outcomes. A major socio-economic limitation of crop protection strategies that rely on plant diversity management is the effect of diversification on the whole economic outcome, both the reduction in production and the savings from reduced input used, which is not well understood or documented in the scientific literature. The available studies indicate that for current agrifood systems, economic return with crop diversification is usually reduced in the short term and economic risk is increased. Both these effects act as a major constraint on adoption. As we expect that most modes of diversification would be implemented by individual farmers, the social benefits for society, of pesticide pollution reduction, enhanced biodiversity and related services, must be translated into appropriate support to promote the adoption of diversification practices. First, the implementation of public subsidies and payments for environmental services should be carefully designed to properly account for all direct and indirect costs, such as the trade-offs among different ecosystem services (Capodaglio and Callegari, 2018). Second, promoting farmer-to-farmer cooperation is another opportunity through collective purchasing of equipment, sharing of labour and developing local exchanges of products (Martin et al., 2016). Participatory research, such as in the selection of varieties and the development of new cropping systems, is another way of developing this sense of cooperation and community among farmers (Berthet et al., 2020). Finally, peer effects will likely play a role where farmers adopt innovative practices only after the example of neighbouring farmers (Schmidtner et al., 2012). Farmer demonstration will therefore be a key element of promoting new modes of plant diversification.

*There is a need for integrated, large-scale studies to analyse interactions between all ecological effects induced by plant diversification, and to assess the feasibility of the deployment of multi-pest crop protection strategies across multiple scales.*Dispersal of organisms across landscape may connect different crops in time and space, linking crop systems together. The management of multiple pests across multiple crop systems and scales remains a major challenge for an agro-ecological transition to sustainable pest control (Litsinger and Moody, 1976). Such complex ecological interactions have crucial implications for the success of plant diversification on pest control, and more broadly, on ecosystem services. However, the hypothesis that landscape re-diversification can restore the biotic interactions that underpin ecological regulations has yet to be tested. Landscape diversity is frequently studied ad hoc by comparing various levels of landscape simplification, rather than expressly through large-scale landscape restoration trials. The degradation of biodiversity and species pools on large (i.e. regional) dimensions, as well as the history of disturbance, extinction debts, and the growing intensity of climate change, may make these goals difficult to achieve (Kuussaari et al., 2009; Lunt and Spooner, 2005).

Considering all agro-ecological and socio-economic determinants of plant diversification implies that we must start testing expectations for pest control at all scales up to landscape scale (Landis, 2017), including their socio-economic organization, in order to challenge the assumptions of pest suppressive landscapes under realistic, and where possible controlled conditions (Begg et al., 2017). Modelling approaches can complement this endeavour, especially through the exploration of scenarios for the deployment of diversification methods, and the selection of promising landscape properties to explore empirically (Tixier et al., 2013). Involving farmers and agricultural stakeholders in the design of agro-ecological landscapes is then a prerequisite (Duru et al., 2015b; Jeanneret et al., 2021; Petit et al., 2020). The goal should be to determine the set of acceptable and effective diversification strategies for each territory, which reflect its social-ecological specificities while also creating the right governance procedures to support the transition (Duru et al., 2015b).

Limitations of this conceptual framework and perspectives.

Literature shows that plant diversification is promising, but the majority of the articles makes it clear that there are many knowledge gaps for its implementation. We believe that the framework is one more step forward.

The ecological limitation of our approach maybe concerns long-distance dispersal pests, which are mainly associated with meteorological factors as air masse fluxes (e.g. Leyronas and Nicot, 2013). However, plant diversification could locally influence these air masse fluxes through the establishment of woody semi-natural elements, while the diversity of interaction networks based on plant diversification could influence their ability to induce outbreaks.

From a socio-economic and agronomic point of view, wheat production and the transformation sector in particular is currently focussed on the criterion of homogeneity of the grains produced. Same constraints of homogeneity are shared by many arable crops, such as processing potatoes or oil seeds. Other systems, such as mixed agricultural and animal production at the farm or the territory level with a portion of local crop consumption, can alleviate some of the obstacles to downstream output (Martin et al., 2016). Human food markets are relying more on contracts, with precise requirements linked to labels and strong traceability issues, whereas animal feed markets are more open (Meynard, 2013). Plant diversity could be deployed using these less constrained production systems rather than cash crops at farm level but also locally through development of local exchanges between arable and livestock farms (Martin et al., 2016; Moraine et al., 2017). However, the upstream channels and public incentives in these alternative systems are sometimes less developed, with extremely little varietal innovation for example (Meynard et al., 2017). It appears to us necessary to go beyond the logic of the crop or the large-scale value chains if we want to support a strong agro-ecological transition.

Finally, the long-term temporal dimension of several decades must be considered in concrete terms to the conceptual framework as climate change and its implications must be addressed (IPCC, 2021). On the one hand, climate change modifies the abiotic conditions for plant growth and development (Ababaei and Chenu, 2020; Asseng et al., 2019; Gammans et al., 2017; Bohan et al., 2022), as well as the conditions for the development of pests and their natural enemies, their geographical distribution and the injury profiles themselves (Bebber et al., 2013; Chaloner et al., 2021; Fones et al., 2020; Monticelli et al., 2022). The management of pests and diseases through plant diversification therefore implies considering climate change and designing systems whose equilibrium will be precarious by nature (even if plant diversification is also an opportunity for resilience to climate change, Dardonville et al., 2020, Marini et al., 2020). On the other hand, farming practices have already adapted to tackle climate warming (shifting cycles as part of an avoidance strategy, irrigation, choice of new species or varieties; Anderson et al., 2020; Raza et al., 2019). Studies have demonstrated the adaptive response of pathogens to temperature by their intra-specific diversity (de Vallavieille-Pope et al., 2018; Mariette et al., 2016). This acclimation of pathogens to temperature, especially for those with a broad geographical distribution and re-emerging worldwide, suggests that we must take account of these patterns of local adaptation to build robust diversification strategies for pest control at the landscape scale.

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