Spatial diversification of agroecosystems to enhance biological control and other regulating services: An agroecological perspective

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Abstract

Spatial diversification of crop and non-crop habitats in farming systems is promising for enhancing natural regulation of insect pests. Nevertheless, results from recent syntheses show variable effects. One explanation is that the abundance and diversity of pests and natural enemies are affected by the composition, design and management of crop and non-crop habitats. Moreover, interactions between both local and landscape elements and practices carried out at different spatial scales may affect the regulation of insect pests. Hence, research is being conducted to understand these interdependencies. However, insects are not the only pests and pests are not the only elements to regulate in agroecosystems. Broadening the scope could allow addressing multiple issues simultaneously, but also solving them together by enhancing synergies. Indeed, spatial diversification of crop and non-crop habitats can allow addressing the issues of weeds and pathogens, along with being beneficial to several other regulating services like pollination, soil conservation and nutrient cycling. Although calls rise to develop multifunctional landscapes that optimize the delivery of multiple ecosystem services, it still represents a scientific challenge today. Enhancing interdisciplinarity in research institutions and building interrelations between scientists and stakeholders may help reach this goal. Despite obstacles, positive results from research based on such innovative approaches are encouraging for engaging science in this path. Hence, the aim of the present paper is to offer an update on these issues by exploring the most recent findings and discussing these results to highlight needs for future research.

Keywords: Agroecology, Ecosystem services, Conservation biological control, Crop diversity, Interdisciplinarity, Transition

1. Introduction

Increasing the environmental sustainability of farming through a reduction of external input uses is a main challenge for today’s agriculture. The concept of agroecology proposes to mobilise ecological processes towards the delivery of ecosystem services (Hatt et al., 2016), i.e. the benefits ecosystems can provide to human well-being (Reid et al., 2005). Pesticides are among these external inputs, for which there is evidence of their harmful effects on human health (Mostafalou and Abdollahi, 2013) and the environment (Annett et al., 2014; Devine and Furlong, 2007). Moreover, their efficiency faces pest resistance (Heap, 2014; Thieme et al., 2010) and consumers call for healthier food (Howard and Allen, 2010). This is leading to ever tighter regulations on their use (Skevas et al., 2013). Hence, programs have been set by governments of countries to reduce pesticide uses (DEFRA, 2013; MAP, 2008). Nevertheless, applying pesticides remains the most common way to protect crops (Hossard et al., 2017), inviting strengthening of efforts at various levels.

One of the propositions put forward by agroecology hinges on the conception of making farming systems less sensitive to pest pressure by mobilising biological regulations in agroecosystems (Malézieux, 2012; Nicholls and Altieri, 2004). *Functional agrobiodiversity* is ‘those elements of biodiversity on the scale of agricultural fields or landscapes, which provide ecosystem services that support sustainable agricultural production and can also deliver benefits to the regional and global environment and the public at large’ (ELN-FAB, 2012). Functional agrobiodiversity, through ecological processes and functions (e.g. predation, flower visits, mineralisation), allows the provision of regulating services (e.g. pest control, pollination, nutrient cycling), on which provisioning (production of biomass for food, fibre and energy) and cultural services (e.g. landscape sight, recreation sources) depend (Zhang et al., 2007). Nevertheless, enhancing agrobiodiversity may also induce disservices (e.g. plant competition, crop herbivory). Intensive agriculture optimizes the provision of biomass while limiting the occurrence of these disservices by simplifying and artificializing agroecosystems with the use of external inputs. These external inputs also decrease the flow of regulating services (e.g. pest control, pollination, water flow regulation, carbon storage) (Foley et al., 2005; Robinson and Sutherland, 2002). The challenge remains in mobilising functional agrobiodiversity able to provide regulating services for producing resources with fewer external inputs and with a limited provision of disservices (Power, 2010; Zhang et al., 2007). However, there is a debate whether functional agrobiodiversity enhances the delivery of ecosystem services through high species richness, or the presence of some key species, or even the involvement of functional traits of individuals (in the case of insects: e.g. Cardinale et al., 2003; Jonsson et al., 2017; in the case of plants: e.g. Hatt et al., 2017c; Uyttenbroeck et al., 2017; for a review: Perovic et al. 2017).

Biological pest control is a regulating service delivered by functional agrobiodiversity (Zhang et al., 2007). Predators and parasitoids can be mobilised to control insect herbivores (top-down control, Gurr et al. 2003). These natural enemies find in non-crop habitats a shelter against adverse conditions, overwintering sites, floral resources, prey and hosts (Gurr et al., 2017). Favouring their presence towards pest control relates to *conservation biological control* (Barbosa, 1998). Plants on which pests feed can moreover be managed (bottom-up control, Gurr et al. 2003). The tactic consists in complicating the ability of pests to locate and develop on their host plant. Because development of specialised herbivores is facilitated in homogeneous fields (i.e. *resource concentration hypothesis* of Root, 1973), diversifying cropping areas by mixing crops (i.e. intercropping), crop with non-crop plants (i.e. cover cropping) or trees (i.e. agroforestry) has been proposed (Altieri and Nicholls, 2004). Enhancing both a bottom-up and a top-down control of insect pests, i.e. considering tritrophic interactions as trophic levels are highly overlapping (Wilkinson and Sherratt, 2016), by spatially diversifying crop and non-crop habitats represents the first two phases proposed by Zehnder et al. (2007) for managing arthropod pests without chemical pesticides in a context of organic farming and is the main component of agroecological crop protection described by Deguine et al. (2016). Although they can be implemented at the farm level, they together induce a diversification at the landscape scale, influencing insects (both pests and natural enemies) that are highly mobile, easily crossing farm borders. Hence, considering the landscape scale, in addition to smaller scales, is essential to understand the pest regulation processes and to design pest control strategies (Tscharntke et al., 2005; Zhao et al., 2016).

These last 10 years, studies highlighted how spatial diversification of agroecosystems can lead to the regulation of insect pests. Efforts have been made in reviewing and synthesising through meta-analyses the numerous studies assessing the effect of spatial diversification at the local and landscape scales on the control of insect pests. In addition, research has continued addressing specific issues, i.e. how to compose, manage and design crop and non-crop habitats at the local scale, and how managements at the local and landscape scales interact. Hence, the first aim of the present paper is to summarize our current knowledge by discussing these recent findings, to highlight gaps and propose issues for future research.

In addition, insects are not the only pests that trouble farmers, and pests are not the only biotic or abiotic elements of the agroecosystem that need to be regulated. Indeed, weeds and pathogens but also soil erosion or nutrient run-off lead to crop losses (Oerke, 2006). Moreover, pollination determines yield and quality of many crops (Bommarco et al., 2012; Holzschuh et al., 2012). Therefore, regulating multiple pests along with favouring the provision of other regulating services is needed. Previous papers addressed this need to develop multifunctional systems (Fiedler et al., 2008; Gurr et al., 2003; Kremen and Miles, 2012; Marshall and Moonen, 2002). Recently, Landis (2017) approached the issue by focusing on levers to trigger at the landscape scale. As studies generally focus on a single regulation (as is discussed in the first part of the present paper), our second aim is to address the issue of multifunctional farming systems, in exploring the possible ways to compose, manage and design crop and non-crop habitats towards the provision of multiple regulating ecosystem services. After Landis (2017), it is proposed here to address the issues at a more local scale, i.e. habitat composition and management as well as field/farm design.

Finally, such an investment of scientific research is only meaningful if it aims at participating in the development of a more sustainable agriculture. Therefore, our third aim is to discuss ways to trigger change so that the existing knowledge on ecological processes can be translated into practice in farmers' fields.

Because conditions of crop and non-crop habitat diversification are very different between temperate and tropical regions, the present perspectives focus on agricultural systems under a temperate climate.

2. Spatial diversification towards biological control of insect pests

2.1 Does spatial diversification at local and landscape scales enhance insect pest regulation?

2.1.1 At the local scale

Diversifying plants in space is possible by cultivating several crops (i.e. intercropping), crop with non-crop plants (i.e. cover cropping), or crop with trees (i.e. agroforestry) simultaneously in the same field, and by implementing non-crop habitats. In a meta-analysis, Letourneau et al. (2011) showed that spatial diversification of both crop and non-crop habitats at the local scale allows reducing insect pests and damages to crops while increasing natural enemies. More specifically, increasing plant diversity tends to enhance abundance of generalist predators, while not affecting abundance of specialist pests (Dassou and Tixier, 2016). Nevertheless, when focusing on specific practices (summarized in Table 1), the effect of diversification may vary. For example in their review, Lopes et al. (2016) showed that diversifying crop habitat solely through intercropping allows significantly reducing pests while not necessarily enhancing natural enemies in wheat (*Triticum aestivum*)-based systems. Such a bottom-up control of pests was also analysed for cover cropping (Médiène et al., 2011). The success of this bottom-up approach (inter- and cover-cropping management) on pest reduction can be explained by the creation of chemical and physical barriers by the non-host plants complicating the search for host plants by pests (Poveda et al., 2008). Moreover, a reason of the non-significant increase in natural enemies could be that such diversified systems do not necessarily provide stable habitats with non-prey resources needed for numerous natural enemies (Lundgren, 2009). Holland et al. (2016) reviewed the ability of a diversity of non-crop habitats in Europe to enhance conservation biological control at the local scale. They reported that linear woody (i.e. hedgerows) and grassy strips (i.e. wildflower strips, beetle banks, naturally regenerated strips) were those mainly studied, generally supporting natural enemies, with however a variable effect on insect pest reduction in adjacent crops. They also highlighted a lack of knowledge regarding other habitat types, such as woodlots and ungrazed pasture that might not be especially managed for biocontrol purposes, but may be abundant in agricultural landscapes.

2.1.2 At the landscape scale

Spatial diversity is considered as the proportion of non-crop area, of natural habitat, of crop or by measuring habitat diversity using indicators such as the Shannon index and the Simpson index. Moreover, the landscape size can vary from small (250 m wide) to large (several km wide) scales (which questions where to situate the frontier between the local and the landscape scale). A meta-analysis based on studies using these indices and considering various scale sizes, reported an overall enhancement of natural enemies when landscape complexity is increased (Chaplin-Kramer et al., 2011). This same analysis specifically highlighted that, although generalist enemies positively responded to landscape complexity, specialist ones were especially enhanced at a small scale (below 1 km). Nevertheless, regarding pest abundance and control, inconsistent results were obtained from different meta-analyses. Chaplin-Kramer et al. (2011) did not find any response of pests to landscape complexity while Veres et al. (2013) reported a reduction of insect pest abundance, hence an increase of their control within fields when the amount of semi-natural areas increases. Specifically on aphids (Hemiptera: Aphididae), landscape simplification (i.e. an increased proportion of cultivated land) also tends to reduce their natural control (Rusch et al., 2016). Chaplin-Kramer et al. (2011) and Veres et al. (2013) proposed explanations for the variable effects of landscape complexity on insect pests across studies. Despite the resource concentration hypothesis (Root, 1973), large fields may favour pest dilution, resulting in a reduced abundance in regard to the field size. Moreover, although non-crop habitats can enhance natural enemies and in turn pest control, landscape complexity may also complicate their search for prey or hosts. The use of insecticides in fields may also vary across the landscape and interfere with the effect of landscape complexity by reducing pest abundance in simplified landscapes. Indeed, a positive correlation between simplified landscapes and insecticide uses was reported (Meehan et al., 2011).

The proportion of crop and non-crop areas remains the main index for measuring landscape complexity. Some studies also consider habitat diversity, assigning functions to these specific areas for insects. This refers to the *compositional heterogeneity*, that can be complemented by the *configurational heterogeneity*, which evaluates the arrangement of the various types of habitats within a landscape (Fahrig et al., 2011). Landscapes with a high configurational heterogeneity can support predatory ladybeetle abundance and diversity (Woltz and Landis, 2014) and more generally a high abundance and diversity of species in crop fields (Fahrig et al., 2015). A high configurational heterogeneity produces long interfaces between crop and non-crop areas. Such interfaces allow natural

Table 1. Types of crop and non-crop habitats with their functions and specificities (i.e. composition and/or management) in regard to control of insect pests.

Habitat	Type	Functions for pest control	Specificities	References
Crop habitat				
Mixing cultivated crops	Intercropping	Complicating the search of host plant for pests	Multiple crop species hosting different pests	Lopes et al., 2015; Ndzana et al., 2014
	Variety mixture	Complicating the search of host plant for pests	Multiple varieties of a given species with different sensitivity to their pests	Grettenberger and Tooker, 2017
Mixing cultivated crops and trees	Agroforestry	Complicating the search of host plant for pests	Usually not managed for enhancing pest control	Muhammad et al., 2005; Stamps et al., 2009
Mixing cultivated crops and non-crops	Cover crop	Complicating the search of host plant for pests	Non-host species, usually not harvested	Dunbar et al., 2016; Irvin et al., 2016
Non-crop habitat				
Herbaceous strip	Wildflower strip	Support of flower-visiting natural enemies	Rich in flowering species	Balzan et al., 2016a; Hatt et al., 2017c; Tschumi et al., 2016b
	Beetle bank	Support ground-dwelling natural enemies	Vegetation structure through selected grassy species	MacLeod et al., 2004; Woodcock et al., 2008
	Naturally regenerated strip	Support ground-dwelling natural enemies	Herbaceous margin at low price	Rouabah et al., 2015
Herbaceous patch	Grassland, fallow	Support flower-visiting and ground-dwelling natural enemies	Usually not managed for enhancing pest control	Werling et al., 2014
Woody strip	Hedgerow	Support flower-visiting and ground-dwelling natural enemies	Multiple habitat types (tree, shrub, grass)	Dainese et al., 2017; Morandin et al., 2014
Woody patch	Woodlot	Support flower-visiting and ground-dwelling natural enemies	Usually not managed for enhancing pest control	Bianchi et al., 2008; Gonzáles et al., 2017

enemies that overwinter in non-crop habitats to migrate into crops (Macfadyen et al., 2015). Nevertheless, non-crop areas can also favour pest colonization (discussed by Tscharntke et al., 2016), thus the effect of a high configurational heterogeneity on pest control remains to be assessed (but see Plećaš et al. 2014).

At both local and landscape scales, spatial diversification of crop and non-crop habitats can reduce insect pest abundance on the one hand, but on the other hand several factors may intervene to create variability in pest control. In this context, current research focuses on how to compose, design and manage crop and non-crop habitats, at both—and between—the local and landscape scales, to enhance insect pest regulation.

2.2 How to compose and design crop and non-crop habitats to enhance insect pest regulation?

Five hypotheses have been proposed to explain why the introduction of non-crop habitats may not lead to pest control in adjacent crops (Tscharntke et al., 2016). One of them is that non-crop habitats are inappropriate in composition or configuration to provide large enough enemy populations needed for pest control.

2.2.1 Composition of non-crop habitats

Species diversity and functional diversity of habitats are two indicators used to assess the effect of habitat composition on pest control. Regarding herbaceous flowering strips, the *pick and mix approach* focuses on the species diversity by assessing the effect of a diversity of flower species on natural enemies (Wäckers and Van Rijn, 2012). Recent field-based experiments highlighted the ability of these tailored flower mixtures to enhance insect pest control and reduce crop damage in the adjacent crops, as compared with the generic flower mixture often proposed in the framework of agrienvironmental policies for biodiversity conservation purpose (targeted pests were aphids on potato [*Solanum tuberosum*] and leaf beetles [Coleoptera: Chrysomelidae] on winter wheat, Tschumi et al., 2016b, 2015 respectively). Additionally, the *functional diversity approach* has been considered, with the hypothesis that mixtures with high functional diversity (i.e. constituted with flower species presenting different values for their traits, Lavorel et al., 2008) support a high diversity of natural enemies. Indeed, different natural enemies are sensitive to different values of traits (e.g. colour, nectar and pollen availability, flowering time and duration, flower volatiles) (Campbell et al., 2010; Fiedler and Landis, 2007a; Hatt et al., 2017b; Wäckers, 2004). Nevertheless, recent findings did not confirm this hypothesis (Balzan et al., 2016a; Hatt et al., 2017c). A reason is that some attractive species present in the mixtures may have overwhelmed the effect of functional diversity. Hence, introducing such attractive flower species in the strips could be efficient, meeting the pick and mix approach.

Hedgerows are another type of non-crop habitat. Their role in supporting natural enemies has been mainly studied in orchards. Nevertheless, their ability to enhance biological pest control has been rarely assessed (Holland et al., 2016). Still, Morandin et al. (2014) reported an increased abundance of parasitoids and a reduced density of pests (i.e. aphids, flea beetles [Coleoptera: Chrysomelidae], weevils [Coleoptera: Curculionoidea] and bugs [Hemiptera: Miridae, Pentatomidae]) in adjacent tomato (*Solanum lycopersicum*) fields. Similar assessment in field crops is needed. The potential of hedgerows to support natural enemies may come from the presence of flowering shrub and herbaceous species (Landis et al., 2000). On the one hand, there is a lack of knowledge on the effect of a variety of tree species on natural enemies and pest control. On the other hand, as the flowering cover often associated with hedgerows may be important (Morandin and Kremen, 2013), the knowledge in the composition of flower mixtures for enhancing pest control presented before may be applied to hedgerow habitats too.

The choice of flower species to compose mixtures must also be based on the optimal time lag between flower appearance, crop growth and insect pest occurrence. In a rotation scheme where crops—thus insect pests—change within and between growing seasons, sowing annual species mixtures presents the advantage of choosing species able to support the natural enemies of the targeted insect pests. For example, to regulate aphids, annual flower species from Asteraceae (e.g. *Centaurea cyanus*, *Calendula arvensis*) and Apiaceae (e.g. *Coriandrum sativum*, *Daucus carota*) families are often considered because they are known to be visited by some of their natural enemies, among others hoverflies (Diptera: Syrphidae), ladybeetles (Coleoptera: Coccinellidae) and parasitoids (Hymenoptera: Braconidae; Aphelinidae) (Campbell et al., 2012; Martínez-Uña et al., 2013; Wäckers and Van Rijn, 2012). Implementing perennial species could also provide benefits, notably offering overwintering sites to natural enemies and favouring their presence at the early stage of insect pest colonisation. Nevertheless, perennial mixtures must allow enhancing a broad variety of natural enemies, able to control the diversity of pests that will follow the rotating crops. Fiedler and Landis (2007b) reported the attractiveness of various species, among them perennials, to natural enemies and recommended a list of species to use (native from Michigan, USA), e.g. *Eupatorium perfoliatum* (Asteraceae), *Potentilla fruticosa* (Rosaceae), *Apocynum cannabinum* (Apocynaceae), *Angelica atropurpurea* (Apiaceae) [see also their website: http://www.canr.msu.edu/nativeplants]. The issue for future research is to assess in fields whether such perennial flowering species can support natural enemies of the pests occurring on crops of a whole rotation cycle.

2.2.2 Composition of crop habitats

The choice of crop varieties has always been a key element to limit damage from insect pests and breeding programs have led to the development of an array of resistant varieties. Increasing intraspecific diversity of a cultivating crop species is another approach for increasing crop resistance to pests: similarly to intercropping, variety mixtures may be constituted of genotypes with different sensitivity to pests, finally complicating the search of appropriate host plants for specific herbivores (reviewed by Tooker and Frank, 2012). However, Grettenberger and Tooker (2017) recently reported inconsistent effects of wheat variety mixtures on aphid suppression (*Rhopalosiphum padi*) observing that the presence of particular genotypes within mixtures, rather than diversity *per se*, allowed reducing aphid abundance. Similarly to testing multiple cultivar mixtures, assessing various crop combinations and their efficiency in limiting insect pest pressure would help in choosing which species should be intercropped.

2.2.3 Design of agroecosystems

The arrangement between crop and non-crop habitats, but also the cropping design itself in the case of intercropping, may be determinant for the enhancement of biological control. Wildflower strips and hedgerows are often introduced at existing field margins, but could also be set within fields, resulting in dividing large fields into smaller parcels and increasing configurational heterogeneity. Successions of wheat crops and wildflower strips or trees, compared solely with wheat, was reported to reduce aphid abundance and support aphidophagous hoverflies and parasitism rate (Hatt et al., 2017a; Muhammad et al., 2005, respectively). As for intercropping, various designs (i.e. ways of combining the crops together) exist (Andrews and Kassam, 1976). In wheat-based systems, strip intercropping generally better favours pest reduction and natural enemy support than mixed or relay intercropping (Lopes et al., 2016).

These findings show that studies on spatial diversification must be accompanied by an assessment of their composition and design in terms of space, but also temporality, to propose systems that indeed enhance biological control (Fig. 1).

2.3 How to manage crop and non-crop habitats to enhance insect pest regulation?

2.3.1 At the local scale

The management of habitats may also affect the ability to support natural enemies and enhance pest control. Mowing of flowering strips (followed by the removal of the biomass) for example is needed to maintain a diversity of plant species (Pfiffner and Wyss, 2004) but it also disturbs the habitats for insects. Hence, it is recommended to reduce mowing frequency (i.e. once a year) (Horton et al., 2003) and to mow only the half of the strip width every year to permanently keep a vegetated area (e.g. the *improved field margins* measure of the Swiss agrienvironmental policy, Jacot et al. 2007). Nevertheless, the presence of unwanted weeds remains an issue for farmers who often spray herbicides locally to destroy them (Haaland et al., 2011). Exploring in which way the mowing regime may help to reduce the occurrence of such weeds is needed. Similar issues exist for hedgerows, for which branches are cut for maintaining the aligned habitat, but where the way they are cut affects the hedge structure and finally the insect populations living in trees. Practices maintaining a significant leaf biomass on trees (e.g. hedgelaying avoiding circular saw) were reported to favour invertebrate abundance (i.e. predators but also herbivores) (Amy et al., 2015). It remains to be assessed whether such a management also enhances insect pest control in the adjacent crops.

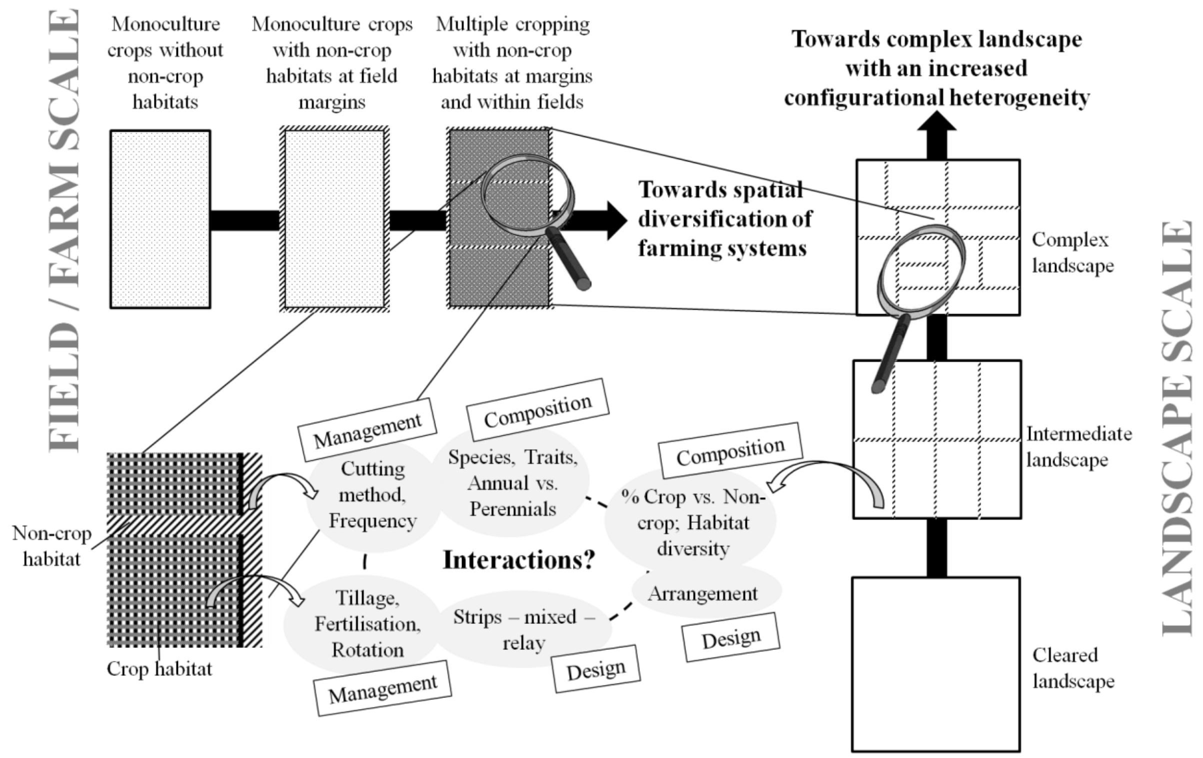
2.3.2 Interactions between local and landscape scale

The way farmers manage habitats on their farms necessarily affects the landscape complexity. According to the *intermediate landscape-complexity hypothesis* (Tscharntke et al., 2012), introducing and managing non-crop habitats at the local scale will be more effective in enhancing biodiversity and ecosystem processes in landscapes of intermediate complexity, compared with simple or complex ones (a concept also developed by Isaacs et al. 2009). Indeed, 'in cleared [i.e. simple] landscapes, the very few species are not a sufficient basis to result in a recognizable response to management changes [and] in complex landscapes, management does not result in a significant effect because biodiversity is high everywhere' (Tscharntke et al., 2005). This hypothesis was confirmed in the case of wildflower strips sown at field margins for enhancing the parasitism of *Plutella xylostella* (Lepidoptera: Plutellidae) and aphids on oilseed rape (*Brassica napus*) (Jonsson et al., 2015). In addition, high plant diversity in wildflower strips along with a complex landscape was found to increase natural enemy diversity and reduce damages from Lepidoptera on tomato crops (Balzan et al., 2016b). Conversely, no interactions between the presence of wildflower strips and landscape complexity were found on ladybeetle abundance and aphid control in soybean (*Glycine max*) fields (Woltz et al., 2012). Finally, Sarthou et al. (2014) observed that the local habitat structure (especially of grass strips), rather than landscape complexity, affects abundance of a diversity of natural enemies at emergence (i.e. after overwintering period) while Dainese et al. (2017) reported that the increased cover of hedgerows at the landscape scale increased aphid parasitism independently from margin diversity at the local scale. This variability of results in the interaction between local and landscape scales may be explained by the diversity of natural enemies, pests and crops studied. Further research continuing evaluating the possible interactions of non-crop habitat management between local and landscape scale is needed to assess whether general trends could finally be drawn or if the local context will remain important. Performing a meta-analysis through the existing body of literature would also be particularly useful for quantifying trends.

Interactions between crop habitat management and landscape complexity on biological control of insect pests have also attracted attention these last years. Reduced tillage at large scales for example, in addition to a high landscape complexity, was found to enhance parasitism of pollen beetles (Coleoptera: Nitidulidae: *Meligethes aeneus*) in oilseed rape fields (Rusch et al., 2011). In addition, reduced tillage can mitigate the detrimental effect of landscape simplification on predation and parasitism of cereal aphids (Tamburini et al., 2016). Indeed, it is assumed that conventional tillage is harmful to ground-dwelling predators and parasitoids that overwinter into the soil (Nilsson, 2010; Soane et al., 2012). The impact of fertilization management, on pest control, also depends on the surrounding landscape complexity. Inappropriate fertilization can affect crop health, with a too low or an excessive provisioning of nitrogen weakening plants (Altieri and Nicholls, 2003). Rusch et al. (2013b) reported on oilseed rape crops that the number of damaged buds by pollen beetles was negatively related to the nitrogen index and positively correlated with the proportion of non-crop habitats. However, in this same study, the abundance of pollen beetles was not determined by the crop nitrogen status, but only by landscape complexity. Finally crop rotation, which allows reducing pest pressure on crops by disrupting the presence of host plants through time (Oerke, 2006), was found to not interact with landscape complexity on cereal aphid parasitism (Rusch et al., 2013a).

As strong dependencies are observed between the management of crop and non-crop habitats and the different scales, additional studies following this vein of research are needed. However, it already appears that multiple agronomic and ecological factors at various scales must be considered simultaneously. Such a comprehensive approach in the study of agroecosystems would imply broadening the scope of insect pest control towards the regulation of various pests simultaneously and the delivery of multiple ecosystem services.

Figure 1. Current issues regarding the impact of diversification of crop and non-crop habitats on pest control: (1) composition, design and management of the habitats at the local and landscape scales and (2) the interactions between these scales.



3. From insect pest control to multiple ecosystem services

3.1 Towards natural regulation of multiple pests

In addition to insect pest control, managing crop and non-crop habitats may allow enhancing natural regulations of weeds and pathogens that are also commonly controlled using chemical pesticides (Fig. 2).

3.1.1 Weeds

Cover cropping leads to substituting unwanted weeds by a manageable plant species (Médiène et al., 2011). The cover crop must be sown to develop earlier than weeds, hence competing for resources and reducing the ability of weeds to grow. Positive results on reducing weed biomass have been reported, even if a negative effect on the main crop yield can also occur (Anderson, 2016; Pfeiffer et al., 2016). When the cover crop is a legume, a recent meta-analysis shows that the main crop yield is not affected (thanks to the ability of legumes to fix and make available the nitrogen for the neighbouring plants) while weed biomass is decreased (Verret et al., 2017). By reducing insect pest abundance on the one hand and weeds on the other hand, cover cropping may provide a double benefit. However assessment of such multiple benefits is still lacking. Likewise, non-crop habitats could also be involved in controlling weeds (Petit et al., 2011) as some natural enemies of insect pests enhanced by semi-natural habitats are also predators of weed seeds, e.g. the majority of carabid (Coleoptera: Carabidae) species (Lundgren, 2009). Even if omnivorous carabids may prefer seeds rather than prey when both are available (Frank et al., 2011), enhancing their survival and activity may allow reducing both insect and weed pests. Beetle banks (i.e. a type of herbaceous strip) can be introduced to support carabids (MacLeod et al., 2004). Evaluating the effect of beetle banks on both insect and weed pests would be useful to identify potential synergies. Moreover, beetle banks could benefit other natural enemies. Particular attention has been devoted to the structure of beetle bank vegetation (large carabid species prefer dense but homogeneous vegetation (Brose, 2003) while smaller ones are positively correlated with heterogeneous vegetation (Rouabah et al., 2015)) but little is known about the benefits they may offer to natural enemies visiting flowers (Ramsden et al., 2015). Hence, a challenge would be to conceive herbaceous strips that optimize both the structure of the vegetation and the provision of flower resources, i.e. mixing the benefits of beetle banks and wildflower strips, to support ground-dwelling predators along with flower-visiting natural enemies, able together to reduce both weed seeds and insect pests.

3.1.2 Pathogens

For fungi, bacteria or viruses, landscape composition and heterogeneity can play an important role in their dispersion. Pathogens are vector-, soil- or air-borne, thus landscape elements act as corridors or conversely as barriers (Plantegenest et al., 2007). At the local scale, Mundt et al. (2007) reported that, whatever the field size, mixing host and non-host plants (i.e. inter or cover cropping) allows limiting the dispersion of the fungi *Puccinia striiformis* responsible for the strip rust on wheat. At the landscape scale, the importance of mixed cropping for limiting disease spread was suggested through modelling (Skelsey et al., 2010). Moreover mixed cropping, by limiting the abundance of insect pests on crops, could be mobilised to control viruses hosted by insects (e.g. aphids, Katis et al., 2007). Lai et al. (2017) reported that variety mixture of tobacco (*Nicotiana tabacum*) allowed significantly reducing aphid (*Myzus persicae*) abundance and incidence of viruses (*Tobacco mosaic virus, Cucumber mosaic virus*, *Potato virus Y*, *Tobacco etch virus*) compared with monoculture. These results are promising for further research studying the effect of intercropping on virus dispersion. As for non-crop habitats, by potentially enhancing top-down predation and parasitism through natural enemies, their implementation could result in a reduction of damage by viruses. However, anti-predation/parasitism behaviour of prey/hosts (e.g. flying, walking away, dropping from the plant), leading to insect pest dispersion, could also favour virus spread. To this dilemma, Dáder et al. (2012) reported a temporal trade-off: in the case of the aphid *Aphis gossypii* facing parasitism, whereas the parasitoid *Aphidius colemani* (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. At the landscape scale, while spatial simplification tends to reduce natural enemies and pest control of aphids (Rusch et al., 2016), Claflin et al. (2017) reported that it also favours the prevalence of the *Potato virus Y* on potato crops. This last result is promising and needs future studies for confirming the interest of landscape complexity in limiting virus spread.

3.2 Towards the provision of multiple ecosystem services

In addition to enhancing the regulation of multiple pests, spatial diversification of crop and non-crop habitats may increase the provision of additional ecosystem services (Fig. 2). This call for multifunctional landscapes is not new but still represents a scientific challenge (Fiedler et al., 2008; Gurr et al., 2003; Kremen and Miles, 2012; Marshall and Moonen, 2002).

3.2.1 Pollination

Flowering habitats can support flower-visiting natural enemies on the one hand, but also pollinators on the other hand (Blaauw and Isaacs, 2014; Nicholls and Altieri, 2013) (some insect species being both natural enemies and pollinators, depending on their development stage, e.g. some species of hoverflies). To benefit both of them, flower mixtures should be adapted to the different ability of insects to feed on flower resources. Campbell et al. (2012) showed that mixtures with both long and short corolla flowers allow supporting parasitoids, hoverflies and bumble bees (Hymenoptera: Apidae: *Bombus spp.*) together, whereas parasitoids did not visit long corolla flowers and bumble bees were absent from short corolla flowers. Nevertheless, several recent studies did not report an increased diversity of flower-visiting insects with such a mixture, recalling that a high functional diversity at the mixture level does not necessarily enhance insect diversity (Balzan et al., 2014, 2016a; Hatt et al., 2017c; Uyttenbroeck et al., 2017). At the landscape scale, however, the increased density of flowering features such as hedgerows showed a positive effect on pest control by parasitoids and pollination (Dainese et al., 2017).

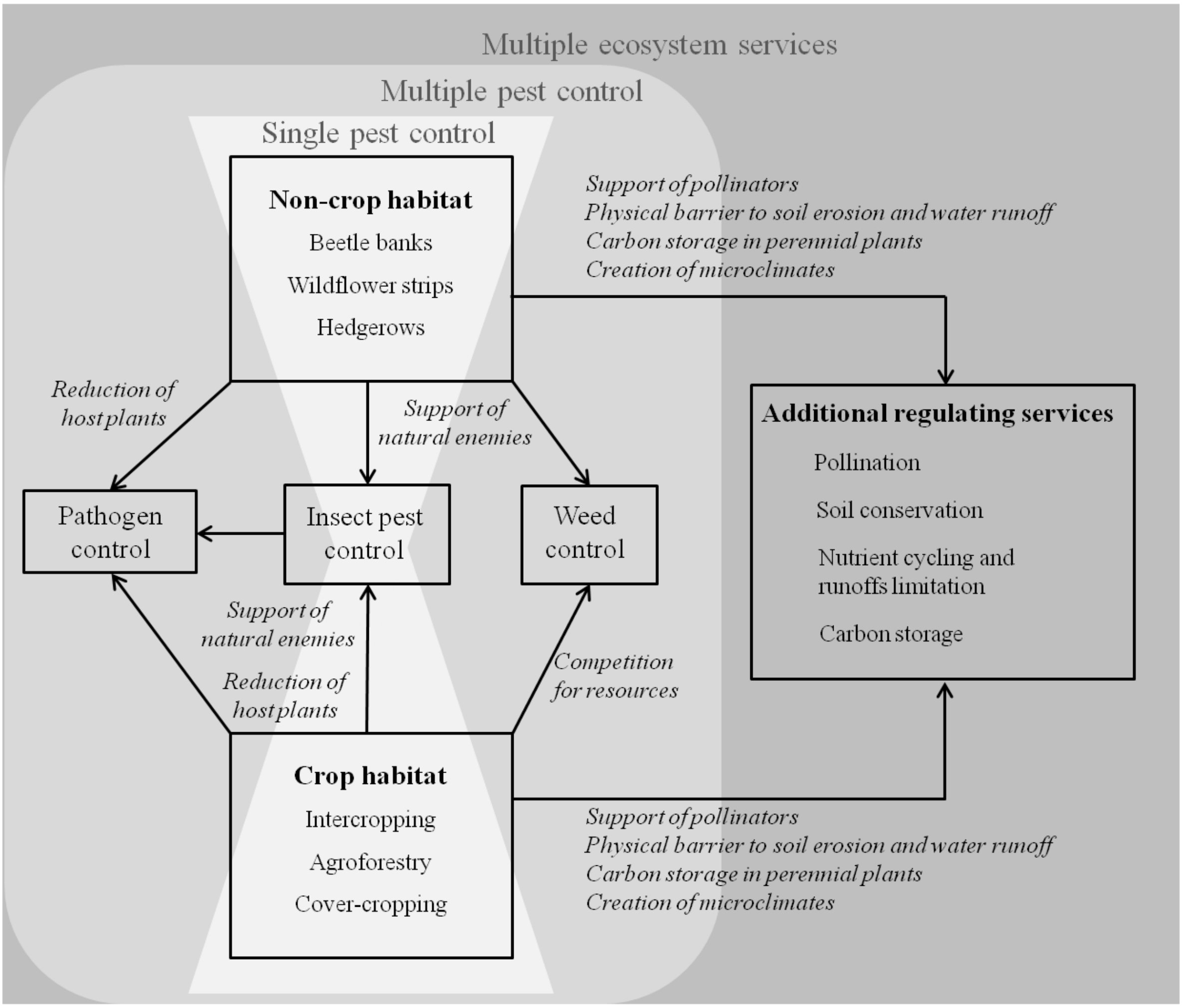
3.2.2 Soil erosion and nutrient run-off

Herbaceous and woody linear habitats could also reduce soil erosion and nutrient run-off (Borin et al., 2010). Nevertheless, buffer strips composed only of grassy species represent little interest for flower visitors, even if they can benefit ground-dwelling predators (Josefsson et al., 2013). Introducing perennial flowering species in buffer strips could support beneficial insects such as pest natural enemies and pollinators, in addition to reducing erosion and run-off (Cole et al., 2015; Gill et al., 2014). ‘Contour farming’, also called ‘contour strip cropping’, is a practice consisting in cultivating successively crop and grass strips in a parcel to reduce soil erosion and nutrient run-off (Panagos et al., 2015; Stevens et al., 2009). Introducing flower resources in these grass strips may also allow supporting flower visitors. Intercropping that provides benefits towards pest control can also lead to an increase of nitrogen and carbon in soils when leguminous plants are combined with cereals, potentially favouring soil fertility and reducing nutrient run-off with fewer fertilizer applications (Bedoussac et al., 2015; Cong et al., 2014). As for agroforestry systems, a recent meta-analysis shows that the introduction of trees generally reduces soil erosion, increases soil fertility and nutrient cycling as well as biodiversity (but the type of biodiversity, hence the functions it can exert, was not specified) (Torralba et al., 2016). The presence of trees within fields would also create a microclimate with potential benefits, but also deficits for ecosystem functioning. Shade due to trees for example, may protect crops from the sun improving their nutritive quality as it was reported for forage species in the USA (Lin et al., 2001), but was also shown to reduce yield of associated wheat in Belgium (Artru et al., 2017).

3.2.3 Biomass production

Biomass production is indeed among the final service and is mostly measured by yield. At the local scale, a global meta-analysis showed a slightly decrease of yield when plant diversity increases in agroecosystems (Letourneau et al., 2011). When more specific practices are considered, reviews reported that an increase of crop diversity through intercropping (Lopes et al., 2016), cover-cropping (Verret et al., 2017) or cultivar mixtures (Tooker and Frank, 2012) tend to maintain crop yield, or to slightly increase it, compared to monoculture systems. The effect of non-crop habitats on yield of adjacent crops has been measured only recently (Uyttenbroeck et al., 2016). Sowing grassy or wildflower strips adjacent to wheat (Tschumi et al., 2016a), bean (*Vicia faba*), oilseed rape (Pywell et al., 2015) or blueberries (*Vaccinium corymbosum*) (Blaauw and Isaacs, 2014) enhanced crop yield by supporting natural enemies and/or pollinators. At larger scales, assessments of landscape diversification on crop yield are also recent (Veres et al., 2013). Schneider et al. (2015) reported no effect of semi-natural habitats on oilseed rape yield but an increase of landscape diversity and complexity increased crop yield in South Korean conventional—but not organic—farms (Martin et al., 2016), suggesting interactions between local management and landscape features on yield.

Figure 2. From the regulation of a single type of pest towards the delivery of multiple ecosystem services through the spatial diversification of crop and non-crop habitats. The processes involved are indicated in italics.



3.2.4 Enhancing synergies

These results show that the composition, design and/or management of crop and non-crop habitats are important for the delivery of multiple ecosystem services. Because certain habitat characteristics may optimize the production of one service, trade-offs may occur when multifunctionality becomes the objective (Power, 2010). Nevertheless, synergies also exist. As mentioned in paragraph 3.1.2, controlling insect pests can allow reducing pathogens when the former is the vector of the latter (Lai et al., 2017). In addition, a well nutrient-balanced soil tends to reinforce plant health, hence their ability to resist pests (Altieri and Nicholls, 2003). Lundin et al. (2013) observed a positive relationship between pollination and pest control resulting in an increased yield. These examples of synergies should encourage the implementation of multifunctional landscapes in an agroecological perspective (Fig. 2). Nevertheless, field- and farm-based evidence is still lacking and conducting such experiments may represent a methodological challenge. Crossing disciplinary barriers, as well as the doors of research institutions, may help taking it up.

4. From theory to implementation, how to trigger change?

4.1 When farmers trigger change

Farmers are the only managers of crop and non-crop areas at the scale of their farm. As recalled before, there is evidence that multiple cropping and the introduction of non-crop habitats can enhance the natural regulation of pests. Nevertheless, there is a variability of results among studies maintaining uncertainties, potentially explaining why implementation in farmer fields remains rare. Indeed many farmers do not have high confidence in such pest control strategies compared with chemical treatments. For example, in the case of flowering strips, few farmers who manage flowering borders for insect conservation in the framework of agrienvironmental schemes acknowledge that these habitats can enhance biological pest control (assumption based on 18 interviews performed in Belgium in 2015, Brédart et al. 2017). Experiments led by scientific institutions can produce knowledge that can help famers to adopt innovative practices. However, experiments conducted by farmers themselves in their farms are known to convince them and their neighbours better (Sutherland et al., 2012).

Brédart and Stassart (2017) recently reviewed the current theories used to analyse changes in farmers' practices. Transition has been described as being a succession of steps (i.e. the 'triggering change cycle' of Sutherland et al. 2012), with different levels of risks (i.e. robust vs. reversible transitions, Lamine, 2011) related to gradual levels of changes (i.e. Efficiency/Substitution/Redesign framework of Hill and MacRae, 1996). Spatial diversification for enhancing the natural regulation of pests may be the final stage of a 'quite slowly and step-by-step' process of change (Lamine, 2011). The author described, for example, the successive changes of a particular farmer as follows: first resistant varieties were adopted and the doses of pesticides were reduced, then date of crop sowing was changed, sowing density as well as fertilizer amount were lowered, and at the latest hedges and buffer zones were created leading to a reduction of plot sizes. Spatial diversification may also be the result of changes that primarily did not aim at reducing the use of pesticides. Vankeerberghen and Stassart (2016) reported the trajectory of farmers for whom questioning soil ploughing pushed to a general reconsideration of biodiversity at the farm level. In these cases, the introduction of diversified cover crops at first led in the end to a general reduction of pesticide uses. It highlights the way farmers experience the potential interactions between different practices and the multiple services a single change can provide (Fig. 2). Studies reporting farmers' trajectories of change show that such a succession is often not planned in advance, but rather a non-linear process with potential returns to previous stages, as well as abrupt changes of direction (Brédart and Stassart, 2017).

Farmers can innovate and engage changes individually. Nevertheless, they also often take part in farmer unions, which facilitate exchanges of information. Working groups—linked or not to farmer unions—can also be organised, where farmers meet for collectively addressing an issue. According to Brédart and Stassart (2017), such working groups help farmers to 'identify the levers of action that each farmer could adjust, change and take over in the specific context of his farm'. Moreover, the group may strengthen farmers in their choice and help them to confront the pressure of a professional environment that is often sceptical towards changes. Reducing pesticide uses may, for example, need a collective change of the conception of what is good farming, the objectives to reach and the indicators used (e.g. considering gross margin instead of absolute yield) (Lamine, 2011). Collective organisations may also attract external experts from various types of institutions (e.g. universities, non-profit organisations, governmental institutions) who bring additional knowledge and advice. Such an opening of the group may even be determinant in its ability to reach its objectives (Dolinska and d'Aquino, 2016). Indeed, farming is intrinsically linked to processing, marketing, distribution and consumption, but also for example to biodiversity conservation, water provisioning, inhabiting, which make complex any process of changes (i.e. *lock-ins* theory, Vanloqueren and Baret, 2008).

4.2 When scientists accompany change

In this context, interrelations between scientists and farmers have been encouraged (MacMillan and Benton, 2014) and conceptualised by scientists as *participatory approaches* (also called transdisciplinarity, collaborative, iterative, action research, Cerf, 2011; Méndez et al., 2013). While farmers experiment, observe and evaluate innovations themselves and progressively engage into the transition process individually and collectively, interactions with scientists allow the latter to consider farmers' constraints and opportunities as well as wishes and objectives in their studies. Such an approach, based on theories and practical experiences, creates a novel type of knowledge that incorporates farmers' constraints. Moreover, scientists may accompany farmers in their interactions with the other stakeholders. Role-playing games could, for example, be used to make stakeholders realise the issues and initiate collective management (such as in Souchère et al. (2010) in the case of run-off management at the landscape level). More generally, workshop meetings and field visits with stakeholders, including researchers, would allow on-site observations and group discussions, finally to build scenarios (Geertsema et al., 2016). Despite a rising interest for participatory approaches, they still represent a challenge for scientists and stakeholders as it asks to use methodologies that change current research practices and would disrupt entrenched farmers' and stakeholders' habits (Cerf, 2011).

Scientists especially would need to broaden their research scope. Indeed, the economic, social and political dimensions fully intervene in farmer decision-making (Cullen et al., 2008; Griffiths et al., 2008), in addition to the ecological and agronomic issues that are multiple and interdependent (Doré et al., 2011). Therefore, enhancing interdisciplinarity (i.e. practices that involve several unrelated disciplines, each with its own contrasting paradigm, Baveye et al., 2014) at the academic level is essential for addressing complex issues related to agricultural sustainability.

Some projects, in both tropical and temperate climate countries, addressing spatial diversification for pest management were conducted recently. For example, in several Southeast Asian countries, flowering strips were introduced at rice (*Oryza sativa*)-field borders to enhance rice pest natural enemies. Field schools were organised to allow farmers and researchers to interact while mass media and entertainment programs were involved to spread information (Westphal et al., 2015). In The Netherlands, the management of already existing ecological landscape elements in the Hoeksche Waard region was adapted so that they also enhance pest control in adjacent fields. While scientists brought knowledge on the effect of semi-natural habitats on natural enemies and pest control, stakeholders (i.e. farmers, nature and landscape conservationists, water managers and politicians) worked together to build strategies with compromises that meet everyone’s interests (Steingröver et al., 2010).

4.3 Economics in the process of change

Interrelations between stakeholders would also allow addressing the economic viability of the transition to sustainability. In studies, the yield is often the main proxy to evaluate the efficiency of innovative agricultural practices (as mentioned in 3.2.3) or farming systems (organic vs. conventional, de Ponti et al. 2012). However, there is no linear relation between yield and income when prices of commodities are unstable. Gross margin does not only depend on income but also on costs, among others, fertilizers, pesticides and fuel, which costs are directly related to a variable price of energy. Yield does not evaluate the efficiency of inputs (i.e. how much is produced per invested capita?) and does not take into account side-effects and pollution costs of chemical input uses on human health and the environment (Tilman et al., 2002).

Economic profitability rather than yield solely may influence farmer choices. However measuring and predicting economic profitability of agroecosystem diversification is not straightforward, as discussed by Griffiths et al. (2008). Modelling has been used to predict the effect of practice changes on economic profits. It showed that with limited changes in terms of farming practices, a reduction of 30 % of the pesticide Treatment Frequency Indicator will not reduce economic profits of farmers in France (Jacquet et al., 2011). Moreover, a prediction showed that the financial investment of sowing wildflower strips adjacent to blueberries was reimbursed from the fourth year after sowing without subsidies (and obviously earlier with subsidies) thanks to the pollination service provided by wild pollinators, but specified that this time frame highly depends on commodity prices (Blaauw and Isaacs, 2014). Additionally in their study, and consistently with the interviews of farmers conducted by Brédart et al. (2017) in Belgium, wildflower strips were sown in marginal lands which highlights that non- or less productive land can be dedicated to non-crop habitats, which represents an opportunity to increase benefits by enhancing ecosystem services without the risk of losing productive lands.

Evaluating economic profits leads to address the importance of political choices for supporting the transition, i.e. economic incentives and regulatory instruments. The efficiency of different incentive tools is discussed (e.g. pesticide taxation, quotas of pesticide use, subsidies) (Jacquet et al., 2011; Skevas et al., 2012). In other words, should farmers alone support the costs? How should public subsidies to agriculture (Hodge et al., 2015) and to research (DeLonge et al., 2016) be used for triggering and supporting changes? What is consumers' and citizens' share (Warner, 2007)? However, it should not be forgotten that farmers' motivations for triggering transition can be diverse and subjective views (e.g. reducing negative effects of their farming practices on the environment) may be as important as the search for economic gains (Stallman and James Jr., 2015).

Building such a comprehensive approach to agriculture needs various views and knowledge backgrounds, as well as gathering together those having different interests within a territory. Whereas the power of pressure groups or lobbies with narrow interests is often accused to prevent transitions towards sustainability (Vanloqueren and Baret, 2009), it is at the core of participatory approaches to enhance a 'democratic process […] in the pursuit of practical solutions to issues of pressing concerns for people, and more generally the flourishing of individual persons and their communities' (Reason and Bradbury, 2001). For scientists, such an innovative way of conducting research—complementary to other methods (Doré et al., 2011)—would allow answering the remaining questions fully (summarized in Table 2) to understand the ecological processes involved to enhance the delivery of ecosystem services in agriculture.

Table 2. Summary of future research needs towards the enhancement of biological control of insect pests, the simultaneous regulation of multiple pests and the provision of multiple ecosystem services through the spatial diversification of crop and non-crop habitats.

Practice	Object to study	Research questions
Towards biological control of insect pests		
Sowing wildflower strips	Composition	Which perennial flower species would allow supporting the diversity of natural enemies able to control the diversity of pests that occur over a whole rotation cycle?
	Management	Can mowing regime help reduce the occurrence of unwanted weeds in mixtures?
Planting hedgerows	Composition	Which tree species are able to support natural enemies and enhance insect pest control in adjacent fields?
	Design	What is the effect of planting hedgerows on insect pest control of adjacent field crops?
	Management	Which cutting regime of trees favours insect pest control in adjacent crops?
Introducing non-crop habitats at the landscape scale	Design	Does a high configurational heterogeneity of landscape enhance insect pest control?
Towards the simultaneous regulation of multiple pests		
Cover cropping	Composition, Design, Management	Can cover cropping reduce both weeds and insect pests simultaneously?
Sowing beetle banks	Composition, Design, Management	Would the enhancement of carabids lead to the control of both weeds and insect pests?
	Composition	Could flowering species be introduced in beetle banks for enhancing both carabids and flower-visiting natural enemies?
Intercropping	Composition, Design, Management	Can intercropping allow the control of both pathogens and insect pests by limiting the spread of diseases, but also virus vectors?
Towards the provision of multiple ecosystem services		
Sowing wildflower strips	Composition	How to compose mixtures that enhance both natural enemies and pollinators?
Sowing buffer strips	Composition, Design, Management	Could a buffer strip both enhance biological control in the adjacent field and limit nutrient run-off as well as soil erosion?
Contour farming	Composition, Design, Management	Could contour farming support both natural enemies, pollinators and limit nutrient run-off as well as soil erosion?
Agroforestry	Composition, Design, Management	Could agroforestry support both natural enemies, pollinators and limit nutrient run-off as well as soil erosion?

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