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Safia Médiène, Muriel Valantin-Morison, Jean-Pierre Sarthou, Stéphane de Tourdonnet, Marie Gosme, Michel Bertrand, Jean Roger-Estrade, Jean-Noel Aubertot, Adrien Rusch, Natacha Motisi, et al.

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Agroecosystem management and biotic interactions: a review

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Abstract Increasing the use of synthetic fertilisers and pesticides in agroecosystems has led to higher crop yields, accompanied by a decline in biodiversity at the levels of field, cropping system and farm. Biodiversity decline has been favoured by changes at landscape level such as regional farm specialisation, increases in field size, and the removal of hedgerows and woodlots. The loss of biodiversity in agro-

ecosystems has increased the need for external inputs because beneficial functions are no longer provided by beneficial species as natural enemies of crop pests and ecosystem engineers. This trend has led to a strong reliance on petrochemicals in agroecosystems. However, many scientists have been arguing for more than two decades that this reliance on petrochemicals could be considerably reduced by a better use of biotic interactions. This article reviews options to increase beneficial biotic interactions in agroecosystems and to improve pest management and crop nutrition whilst decreasing petrochemical use. Four agronomic options are presented. First, it has been shown that the choice of cultivar, the sowing date and nitrogen fertilisation practices can be manipulated to prevent interactions between pests and crop, in either time or space. Nevertheless, the efficacy of these manipulations may be limited by pest adaptation. Second, beneficial biotic interactions may result from appropriate changes to the habitats of natural enemies and ecosystem engineers, mediated by soil and weed management. Here, knowledge is scarce, and indirect and complex effects are poorly understood. Third, changes achieved by crop diversification and, fourth, by landscape adaptation are promising. However, these practices also present drawbacks that may not necessarily be outweighed by beneficial effects. Overall, these four management approaches provide a powerful framework to develop sustainable agronomic practices.

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1 Introduction

Cropping systems must be continually adapted to meet farmers' needs and new objectives in a changing socioeconomic context (Boiffin et al. 2001). Modern agriculture, which was developed to increase productivity to meet demands for food and fibre, has led to an oversimplification of crop diversity at the field, cropping system, farm and landscape levels, with increasing reliance on petrochemical inputs and decreasing use of beneficial biotic interactions (Altieri 1999; Stoate et al. 2001). There is growing evidence to suggest that natural habitat fragmentation due to changes in land use and high levels of agrochemical inputs in crop fields are major causes of the rapid decrease in general biodiversity in many

agricultural landscapes (Robinson and Sutherland 2002; Benton et al. 2003; Bianchi et al. 2006; Farwig et al. 2009), potentially threatening the provision of some services, such as biological pest control and pollination, whilst having a neutral effect on other functional groups. Agroecosystems thus have very low levels of biodiversity, and increasing diversity would probably add complementary elements and increase agroecosystem functioning and sustainability (Gurr et al. 2003; Moonen and Bàrberi 2008). The intensification of arable farming has also had an impact on the other compartments of the environment: soil, water and air (Anonymous 2005; Le Roux et al. 2008). The economic rationale has now been overtaken by environmental issues of concern to society as a whole, and by a new social context, supported by environmental policy and a social demand for more environment-friendly agriculture. Some farmers are currently experimenting with different production systems based on fewer chemical or mechanical inputs, for economic (high input costs), agronomic (pest resistance to pesticides) or environmental (soil erosion, water pollution, biodiversity loss) reasons (Warner 2007). For both these farmers and agronomists, a key question is: how can we decrease petrochemical inputs in agroecosystems to limit their impact on the environment whilst maintaining the productivity and/or profitability of agriculture?

The relationships between biodiversity and agroecosystem functioning are complex and require clarification for each of the services biodiversity can provide. Their positive effects depend principally on interactions between biotic components or between biotic and abiotic components of the agroecosystem, hereafter referred to simply as biotic interactions (*sensu lato*). These biotic interactions are of interest in agriculture for a number of reasons, including the services they provide through non-chemical pest control and improvements in crop growth conditions (resulting from changes in soil nutrient availability and soil structure; Shennan 2008). Our aim in this review was to explore the extent to which and the ways in which it is possible to manage agroecosystems so as to enhance beneficial biotic interactions and decrease the use of petrochemicals. The list of ecological services and environmental consequences of agroecosystem management considered here is not exhaustive, as we focus on crop protection and nutrition but they are the most important processes for maintaining crop productivity and stability. We also limit our review to temperate cropping systems, although most of the principles presented could also be applied to the management of tropical agroecosystems.

The level at which biotic interactions should be managed remains unclear as conflicting results have been published. For instance, the services delivered by beneficial predators may depend on the morphological, anatomic or metabolic characteristics of the crop plant, which may facilitate or hinder their activities. Chang and Eigenbrode (2004) and

Rutledge and Eigenbrode (2003) showed that the predatory efficacy of the ladybird *Hippodamia convergens* against pea aphid, *Acyrtosiphon pisum*, depends directly on the thickness of the wax cuticle in peas. If the wax is too thick, it decreases the adhesion of the ladybird to the leaves, decreasing the speed of prospection or inhibiting prospection altogether. Other natural enemies, such as spiders of the *Linyphiidae* family or hoverfly larvae, may take over this role of predation because their movement on leaves is not hindered by the smooth surface of a thicker wax cuticle. This clearly demonstrates the importance of plant/insect interaction and complementarity between beneficial species (Schmaedick and Shelton 2000). An understanding of these processes, based on the interactions of organisms in food webs, makes it possible to manage them directly (by favouring certain organisms) or indirectly (by modifying environmental conditions favourable to certain organisms), at the crop genotype level. Landscape organisation has been shown to play a very important role as the biological cycle of pests and natural enemies may take place at a scale larger than the individual field (in non-crop areas, for example). Landscape characteristics may also favour or hinder dispersal and colonisation by these organisms in agroecosystems. Metapopulation theory, which has been well developed in ecological approaches, could be used to identify the landscape characteristics and/or spatial deployment of cropping practices most likely to reduce the risk of invasion and persistence of pests in the landscape or to increase the probability of invasion and persistence of biocontrol agents.

We consider here four types of agroecosystem management that might improve the use of beneficial biotic interactions: (a) a single operation/technical choice (e.g. sowing date, fertilisation rate or choice of crop species sown) for preventing the spatial and temporal synchronisation of crop and pests, (b) a set of techniques altering the environment of living organisms at the field scale, (c) the diversification of crop rotation through the introduction of a cover crop and (d) characteristics of the local or regional environment (from hedge management to the spatial organisation of crops and non-crop habitats). At each level, a non-exhaustive analysis of the typical biotic interactions involved and their impact (direct or indirect) on biological pest control and crop growth conditions was carried out to identify the main advantages and limitations of management at these scales.

2 Modifying single practices to prevent the spatial and temporal synchronisation of crop and pests

Starting from current cropping systems, it might be possible to reduce pesticide use by modifying individual practices to separate the crop from pest populations either in space or in time. Indeed, cropping practices influence the ability of the

plant to attract or to repel pests and the synchronisation of crop and pest life cycles.

2.1 Effect of sowing date on synchronisation of the life cycles of the pest and the crop

One of the basic principles underlying pest avoidance is the desynchronisation of crop susceptibility and the biological cycle of various pests (Meynard et al. 2003). In this case, a decrease in biotic interactions (between crop and pest) is beneficial for crop production. For instance, early sowing dates have been shown to reduce the injuries caused by *Leptosphaeria maculans*, the causal agent of phoma stem canker on oilseed rape (Aubertot et al. 2004). In this pathosystem, injury at harvest is most severe if infection occurs soon after emergence (Brunin and Lacoste 1970). As the primary inoculum of *L. maculans* generally peaks between September and December (West et al. 2002), crops sown early have a statistically lower risk of being infected just after their emergence than oilseed rape crops sown later.

Plant pathogens are not the only organisms with a biological cycle related to the crop cycle. For example, some weeds can germinate and emerge at any time in the year (e.g. *Geranium* spp., *Raphanus raphanistrum* L.), whereas others have preferential periods of emergence. For instance, *Adonis aestivalis* L. and *Alopecurus myosuroides* Huds. preferentially germinate and emerge during autumn or winter, whereas *Atriplex patula* L. and *Chenopodium album* L. preferentially germinate and emerge during spring (Bailly et al. 1977). Using this life cycle trait, Chauvel et al. (2001) tested several alternative cropping systems for controlling *A. myosuroides* that had acquired resistance to herbicides of the FOP chemical family (aryloxyphenoxy propionates). One of the most efficient methods for controlling the resistant weed was found to be the introduction of spring crops into crop rotations that previously included only winter crops. Indeed, the introduction of spring crops led to the soil tillage in the spring, destroying weeds that had emerged during the winter.

Animal pests are also susceptible to temporal shifts, creating an offset between their life cycle and the crop cycle. For instance, late-sown winter cereals are less susceptible to cereal aphids (principally *Rhopalosiphum padi* (L.)), which carry the nonspecific barley yellow dwarf virus (BYDV). Maize constitutes a major reservoir of both the virus and its aphid vectors (Vialatte et al. 2006); as it matures, aphids (which may be infected) move in search of green hosts, often early-sown winter wheat or barley. Thus, the late sowing of winter cereals (about 2 weeks after the usual sowing date) or the early sowing of spring cereals reduces BYDV damage because plants emerge and complete the highly vulnerable seedling stage of development whilst temperatures are too low for aphid activity.

2.2 Effect of cultivar choice and nitrogen fertilisation on pest attraction/repulsion and resistance to diseases

Fine-scale identification of the determinants of insect–plant interactions is often used to develop sustainable pest management strategies (Pickett et al. 1997). Certain types of insect behaviour, such as host searching, food finding and oviposition, are known to be affected by visual signals, such as colour, size, leaf structure, plant architecture and chemical signals. The chemical cues from plant that affect the behavioural responses of insects are classified into several categories, including attractants, arrestants, stimulants, repellents and deterrents (Ahuja et al. 2010). We will deal here with attractants, which orient insects towards the source, and repellents, which orient insects away from the source. Several studies have investigated the ways in which plant characteristics affect not only the behaviour of herbivore insects but also that of their natural enemies and the ways in which attraction or repulsion can be used to decrease insect survival. These plant characteristics may be modified by several practices, including the choice of variety and fertilisation.

For example, the host searching and oviposition behaviours of various oilseed rape pests are known to be affected by morphological and olfactory signals. Common pollen beetles (*Meligethes aeneus* F. and *Meligethes viridescens* F.) are attracted by the yellow colour of the flowers and by degradation products of glucosinolates (isothiocyanates; Free and Williams 1978). They have also been shown to adjust the number of eggs laid per bud and the amount of resources allocated to each egg for larval development as a function of the potential capacity of the plant to meet the needs of the larvae (Hopkins and Ekbohm 1996, 1999). Ulmer and Dosdall (2006a) assessed the effects of eight different Brassicaceae species on cabbage seedpod weevil (*Ceutorhynchus obstrictus*) behaviour. They found that the cabbage seedpod weevil preferred *Brassica carinata* for feeding and oviposition. Larval development occurred most rapidly on *Brassica rapa* and larval weight was highest on *Brassica napus*. These authors also demonstrated that high levels of specific glucosinolates were associated with longer development times or lower weight, demonstrating the effects of chemical signals on pest populations. Another pest of oilseed rape crops, the cabbage root fly (*Delia radicum* (L.)), has also been shown to select the most favourable plants for oviposition on the basis of stem diameter (Dosdall et al. 1996; Valantin-Morison et al. 2007). Various studies have shown that the host location and feeding behaviour of the cabbage root fly and the diamondback moth (*Plutella xylostella*) are oriented by glucosinolates and volatile isothiocyanate compounds (de Jong and Städler 1999; Hurter et al. 1999; Renwick et al. 2006). In cereals too, the selection of a host plant by pests

such as the wheat stem sawfly (*Cephus cinctus* Norton) is known to be influenced by plant height, developmental stage and the volatile compounds released by wheat (Piesik et al. 2008). Moreover, differences in natural enemy populations are also observed between species or cultivars. For example, Jönsson et al. (2005) demonstrated that the observed differences in the temporal occurrence of three parasitoid species attacking pollen beetles reflected differences in their response to olfactory and visual plant stimuli. Finally, direct defence mechanisms may be constitutively present or induced upon aphid attack, potentially resulting in significant differences in aphid survival between cultivars (Broekgaarden et al. 2008). In such cases, proteins and secondary metabolites with direct defensive effects, such as lectins and protease inhibitors, may have an antibiotic effect on aphids. Furthermore, the antixenosis and antibiosis properties of certain varieties of wheat against aphids act in synergy with the natural enemies of aphids. Bhuiyan and Wratten (1994) showed that a larger proportion of aphids fell to the ground from awned wheat varieties than from awnless wheat varieties. Similarly, Gowling (1988) found that the visit of a natural enemy to an aphid colony resulted in the fall of a significantly larger number of aphids from a semi-resistant wheat cultivar than from a susceptible wheat cultivar. Gowling and van Emden (1994) provided insight into a complementary mechanism operating in this type of situation. Following the fall of the aphid from the leaf, significantly fewer aphids try to climb back up semi-resistant varieties than susceptible varieties, increasing the likelihood of predation by ground-dwelling polyphagous predators (Losey and Denno 1998). All these studies provide evidence that the morphological and chemical characteristics of the plant play an important role in host selection, oviposition behaviour, survival and subsequent crop damage.

Thus, innovative management measures involving cultivars or species of different attractiveness and repulsiveness can be used in a stimulo-deterrent diversionary strategy. Push–pull strategies are used to repel the pest from the resource (i.e. commercial crop fields), using stimuli that elicit host plant finding, and to attract pests to trap crops (usually in field borders) using attractive stimuli (Cook et al. 2007). Trap crops may be attractive to pest populations because their growth stage, architecture, cultivar or species is favourable. For example, turnip rape has been found to be a preferred host plant for several oilseed rape pests in both laboratory and field conditions (Hokkanen 1989; Nilsson 1994; Cook et al. 2002, 2006; Valantin-Morison and Quere 2006). Barari et al. 2005 have also demonstrated the trap effect of turnip rape on the pest *Psylliodes* and on natural enemies. The trap crop effect of turnip rape is effective when both species have closed buds, but not when both species are flowering.

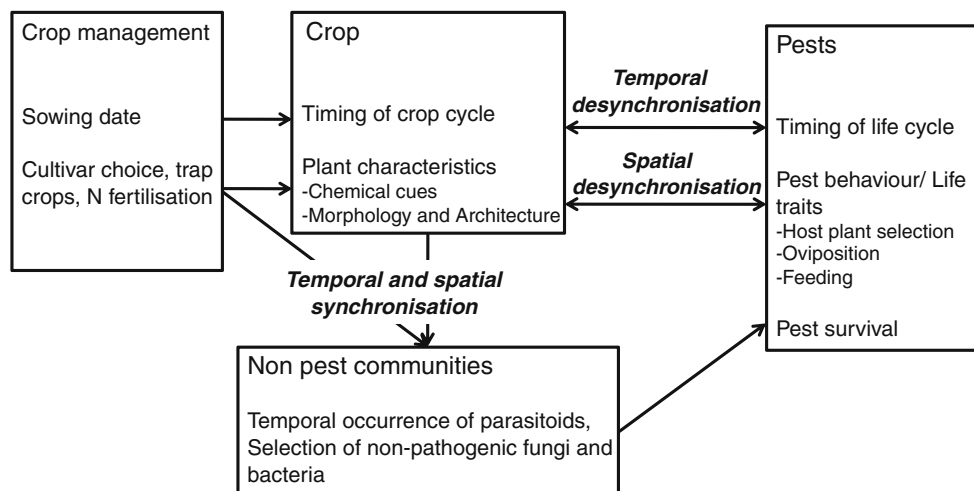
The amount and timing of nitrogen application may have a major effect on the attractiveness of the crop to pests by modifying plant chemical cues and architecture. Nitrogen fertilisation affects the glucosinolate content of the seeds (Milford and Evans 1991) or aerial parts (Markus et al. 1996) of cruciferous crops. The application of large amounts of nitrogen may induce the production of large flower buds, providing more favourable conditions for female pollen beetles. However, high levels of nitrogen fertilisation also result in the production of larger numbers of secondary racemes, enabling the plant to compensate for pollen beetle attacks. Increasing the availability of nitrogen to crop plants may have different effects on different types of pests. Higher levels of nitrogen nutrition favour sap-sucking pests over leaf grazers. Fertiliser application increases the concentration of chemical compounds in cell vacuoles, making plant tissues less appetising and less digestible (Mattson 1980). Leaf grazers ingest plant tissues in their entirety, including the vacuoles (Letourneau 1988; Funderburk et al. 1994; Altieri and Nicholls 2003), whereas sap-sucking pests insert their stylets between cells to reach the phloem, avoiding the vacuoles and the potentially harmful chemical compounds they contain (Mattson 1980).

Plants harbour many non-pathogenic fungi and bacteria, both above and below ground, providing protection against diseases. Endophytic fungi, which colonise plant leaves without causing symptoms, have been shown not only to improve biotic (herbivores) and abiotic (mineral and drought) stress resistance in grasses (Malinowski and Belesky 2000) but also to increase resistance to airborne diseases (Arnold et al. 2003). The efficacy of endophytes could potentially be improved by plant breeding as host genotype influences endophyte species richness and community composition (Pan et al. 2008). The antagonistic effects of some bacterial and fungal species against soilborne diseases (particularly for the genera *Pseudomo-*

nas, *Bacillus* and *Trichoderma*) have long been recognised, and the suppression of particular diseases by the soil is observed after the continuous cultivation of some crops, as for take-all in wheat (Hornby 1998). It has been suggested that the defence strategy developed by plants against soilborne pathogens may involve rhizosphere microorganisms (microorganisms closely associated with roots) antagonistic to these pathogens (Cook 1995). Indeed, the composition and function of the rhizosphere microorganism community are controlled by root exudates specific to particular plant species (Fuente et al. 2006; Broeckling et al. 2008), or even particular cultivars. Thus, the use of varieties able to sustain large populations of microorganisms and/or to select antibiotic-producing microorganisms may decrease the risk of root diseases.

Figure 1 summarises the desynchronisation effects achieved in time and space by modifying the attractiveness and repulsiveness of the crop to pests. Even modifications to single practices, such as those discussed in this section, may provide an opportunity to reduce the injury caused by pests. Crop/pest desynchronisation in time is a simple but effective measure. Unfortunately, several recent changes in crop management have instead synchronised crop and pest cycles. This is the case, for example, for winter cereal production, for which earlier sowing dates have been introduced in Western Europe to maximise radiation interception. Knowledge is accumulating about the molecular aspects of crop–pest interactions, in addition to the ecological aspects. This knowledge provides a source of innovations for the design of new crop management systems. However, there are four limitations to this first type of action. First, some of the biological processes involved are far from simple, and their positive mobilisation may require parameterisation of the effects of cropping techniques. Second, if systematically used, these approaches may cease to be effective due to pest adaptation. Third, there are clearly

Fig. 1 Summary of changes to single practices for preventing the spatial and temporal synchronisation of the crop and pests



interactions between crop management techniques, limiting the effects of single techniques. Finally, conflicts may occur at farm level. For example, organisational constraints may limit the choice of sowing date, and quality objectives may limit the choice of varieties.

3 Modifying the environment of living organisms at the field scale to enhance biological pest control and nutrient use efficiency

Many technical solutions have been envisaged for the management of crops so as to provide a more favourable environment for beneficial organisms, the natural enemies of pest species and ecosystem engineers (Jones et al. 1994) which have effects on the physical and chemical environment favouring nutrient influx into the crop.

In Section 3.1, devoted to pest control, we provide two examples of such solutions. The first, the effect of the tillage system on soil biota and organism habitat, is based on considerable amounts of experimental data; conversely, the use of weeds for natural pest control is an almost entirely new field of investigation. In Section 3.2, we focus on the effect of soil management on earthworm habitat and communities in cultivated fields as a means of enhancing nutrient use efficiency. Earthworms are a key species of ecosystem engineers.

3.1 Effects of no-till systems and weed control on organism habitat and interactions between pests and natural enemies

Soil tillage practices affect organic matter composition, soil moisture and the structure of the soil surface (Holland 2004). In particular, a mulch is formed in the absence of tillage. Several studies have shown that the accumulation of organic matter at the soil surface almost always leads to an increase in the diversity of generalist predators (ground beetles, spiders and rove beetles; Hanna et al. 2003; Mathews et al. 2004; Schmidt et al. 2004; Pullaro et al. 2006). This diversity seems to depend directly on ascending control by saprophagous communities of springtails (Chen and Wise 1999; Ferguson and Joly 2002). This often leads to a decrease in the populations of certain crop pests, such as aphids, caterpillars and Colorado beetle (Zehnder and Hough-Goldstein 1990; Brust 1994; Schmidt et al. 2004; Pullaro et al. 2006). According to Landis et al. (2000), the presence of decomposing organic matter at the surface of the soil provides the predators with alternative prey when there are no crop pests present in the plot. Kendall et al. (1991) even showed, in winter barley crops, that the amount of straw remaining at the soil surface was positively correlated with the diversity of polyphagous predators and negatively correlated with BYDV infection levels (due to

greater predation on vector aphids by these predators). A similar phenomenon was observed following the application of organic matter to plots (Landis et al. 2000). Weed populations may also decrease in size in the presence of a mulch due to an increase in the number of seed-eating ground beetles (Harrison et al. 2003; Pullaro et al. 2006). Furthermore, the presence of sufficiently large amounts of residues after the harvesting of the crop creates an unfavourable environment for weed germination and establishment. Annual weed species with small seeds requiring light for germination are the most sensitive to surface residues, whereas large-seeded annual and perennial weeds are fairly insensitive (Teasdale and Rosecrance 2003). Weed suppression effects decrease during the course of the season as the residues decompose. However, mulch application may also have a negative effect on the crop, by increasing slug populations, for example (Mabbett 1991).

Weed management in low-input or organic cropping systems leads to changes in the number and diversity of weeds present in the plot (Hyvönen et al. 2003; Hyvönen 2007). Several studies have shown that leaving some weeds may make it possible to decrease the abundance of crop pests. This decrease results from an increase in regulation by natural enemies as weeds can provide these enemies with resources, some of which are weed-specific, such as pollen and nectar, alternative prey and hosts (Andow 1990; Häni et al. 1998; Norris and Kogan 2005). However, weed flowers may also attract certain pests, such as common pollen beetles (*M. aeneus* and *M. viridescens*), seeking to feed on flowers after their emergence from winter oilseed rape and before their departure for overwintering sites (Balachowsky 1962).

3.2 Effects of soil management on earthworm habitat and communities: consequence for nutrient use efficiency

Attention is increasingly being paid to the soil macrofauna due to its major contribution to nutrient cycling in agroecosystems. We illustrate this role of ecosystem engineers, with the example of earthworms, considering their major effects on soil fertility and the effects of crop management on their populations.

Earthworms are particularly important for nutrient cycling because they decompose organic matter (Edwards and Bohlen 1996) and increase the availability of some mineral elements (phosphorus, for example). Earthworms also affect soil structure and microbiological activity. The channels they create increase soil porosity (Lavelle 1997) and infiltration, favouring root development (Jégou et al. 2002). Through their burrowing activities, earthworms mix the various soil horizons and help incorporate organic matter into the soil (Cluzeau et al. 1987). Earthworm activity also increases the microbial biomass (Cluzeau et al.

1994; Aira et al. 2003), thus affecting the mineralisation of organic matter. Depending on the ecological group to which they belong, earthworms have different effects on soil structure: anecic worms form large subvertical tunnels, endogeic worms burrow more horizontally quite close to the surface, and epigeic worms remain at the surface and thus have no effect on soil structure. Similarly, the effects of these groups on the fate of crop residues are different: endogeic species are geophagic and ingest already decomposed organic matter, whereas anecic and epigeic species feed on the organic matter at the soil surface.

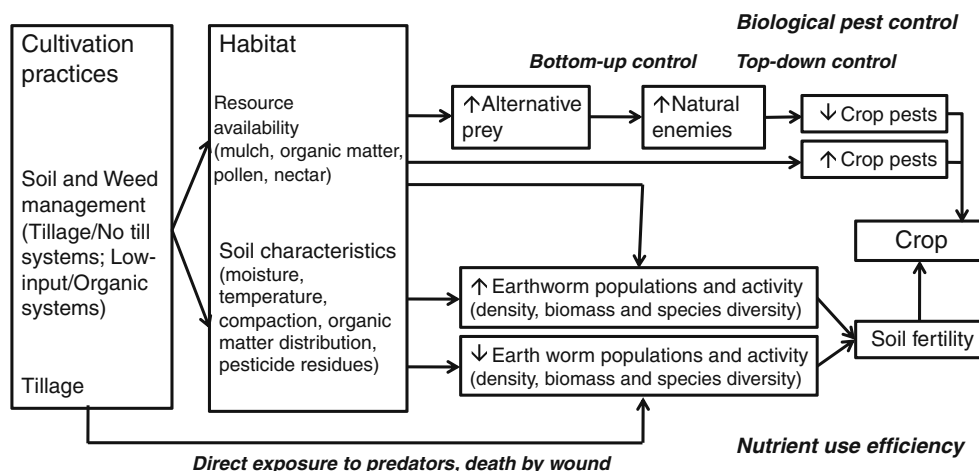
Thus, earthworms improve several aspects of soil fertility, both physical and chemical, and this is beneficial for plant growth. In controlled conditions, it has been shown that the presence of earthworms has a positive effect on plant growth. Scheu (2003), reviewing 83 studies, concluded that 79% showed a positive response to the presence of earthworms, with only 9% showing a negative response and no significant effect in 12%. However, it is more difficult to demonstrate such a response in field conditions because populations are often much smaller than those used for experimentation in the laboratory. In some cases, earthworms can be introduced directly into the field, which has a positive effect (Scheu 2003). However, major differences between species are observed (Shuster et al. 2003), and the fate of the introduced worms must be studied before this technique is applied to commercial fields (Nuutinen et al. 2006). In the meantime, it is possible to favour earthworm populations and their activity through crop management.

Earthworm populations are affected principally by temperature and humidity (Whalen and Parmelee 1999; Pelosi et al. 2008). Food resources are also an essential factor determining the average number of earthworms present in a given soil (Curry 1998). The addition of organic matter to the soil favours earthworm populations (Anderson et al. 1983). Conversely, decreases in organic

matter levels have a negative effect on populations (Mele and Carter 1999; Hendrix et al. 1992). Leroy et al. (2007) compared farmyard manure, cattle slurry and various composts and also reported a slight effect of the quality of the organic matter, and Scown and Baker (2006) observed differences in the abundance of earthworms exposed to dung from various farm animals. The distribution of organic matter also influences the relative abundance of the different ecological groups in the community. Thus, soil tillage, particularly ploughing, is clearly the technique with the strongest impact on earthworm populations (Chan 2001). Ploughing influences earthworm populations not only by changing the distribution of organic matter, but also through other reported effects: death of earthworms directly wounded by the plough, destruction of earthworm habitats and exposure to predators. Anecic earthworms are more affected than endogeic species, which benefit from the burial of the surface organic matter (Nuutinen 1992). Ploughing therefore affects earthworm population density, biomass and species diversity. A negative effect of soil compaction has been reported (Langmaack et al. 1999), although this effect is less frequently described. The passage of vehicles in wet conditions may have a direct effect on earthworms located under the wheel tracks as worms tend to come up to the surface in such conditions (Buck et al. 2000). Negative effects of pesticides have also been reported in some cases, with a high level of variation (Edwards and Bohlen 1996) as a function of the type of active ingredient, the climatic conditions during spreading and the earthworm species considered. Epigeic worms, which live at the surface, are more exposed to pesticides than anecic and endogeic species.

Thus, several crop management techniques have positive or negative effects on earthworm populations. However, techniques cannot be considered separately and the effects on earthworm populations of the entire cropping system must be studied. Pelosi et al. (2009), in a study of several

Fig. 2 Illustration of approaches to the manipulation of organism habitat so as to modify biological pest control and nutrient use efficiency



cropping systems with different levels of productivity, intensities of soil tillage and pesticide use, showed a clear effect of cropping system on the composition of ecological group communities. Anecic worms were favoured by a direct drilling system with the maintenance of permanent crop cover throughout the year, whereas endogeic worms tended to be favoured by conventional crop management (including pesticide use and ploughing) and in the organic cropping system (with mouldboard ploughing). The rationale of cropping systems aiming to preserve or maintain earthworm populations is based on two main elements: increasing carbon resources and managing soil structure, with tillage as limited as possible, whilst avoiding soil compaction. Different means of achieving the objective of maximising carbon return to the soil exist: the application of manure is an obvious method, but it is also possible to keep crop residues in the field whenever possible. Another way of increasing carbon resources for the macrofauna is to maximise carbon fixation by photosynthesis through high levels of production and avoiding periods of bare soil by planting cover crops (see Section 4). It is also possible to introduce temporary grasslands, covering the soil for several years, into the crop rotation. It is not always possible to avoid deep soil tillage, especially ploughing, due to the large number of functions of this operation (weed management, water circulation, decompaction). However, a better knowledge of the dynamics of earthworm populations, possibly based on models such as that presented by Pelosi et al. (2008), makes it possible to optimise the schedule of tillage operations, thereby minimising their impact on earthworm populations. For example, interventions may be scheduled to coincide with periods during which earthworms are less susceptible, such as diapause, particularly during cold periods.

Figure 2 summarises the effects of crop management on habitats, for the pest management and improved nutrient use strategies, outlined in this section. Many studies have already focused on the effect of tillage (or no tillage) on pests and their natural enemies. Both negative and positive effects have been reported, and further research is required to establish the balance between these effects. However, several items have now been evaluated to help farmers evaluate the balance between benefits and risks when they stop ploughing, for example. The situation is very different when considering the effect of weed management on natural pest control. Few empirical or theoretical data are available. Many farmers are used to trying to eradicate weeds from their fields and are not accustomed to consider the role of weeds in establishing habitats for natural enemies (or for controlling pests). Furthermore, most agronomic research is based on experimental data acquired in plots from which weeds are carefully removed. These two examples clearly illustrate the imbalance in our

knowledge of the effects of cropping practices on beneficial biodiversity. These effects are least well known for more indirect methods, opening up new avenues of research. Both the positive effects of earthworms on some of the major processes underlying nutrient availability and the main drivers of earthworm abundance (tillage and the supply of organic matter to the soil) are now well documented. However, these effects are poorly quantified, and little is known about the effects of earthworm species and age. It therefore remains difficult to provide farmers with support for decisions relating to practices. When is it appropriate to till the soil or to weed? How much organic matter should be supplied, and when? Is it better to bury the residues or to leave them on the surface?

4 Introducing a cover crop to modify biotic interactions in agroecosystems

The introduction of a cover crop is an example of the third type of agroecosystem modification considered in this paper: managing crop rotation and diversification. Cover crops, which are not generally harvested, can improve resource availability and the growth conditions of the crop or decrease the impact of pests. Cover crops fall into two categories: (a) annuals grown during an off-season that are killed before planting a cash crop, providing a mulch (some of the effects of which are described in Section 3.1), and (b) living mulches that grow at the same time as the cash crop, for all or part of the growing season, resulting in an intercropping system.

4.1 Effect of a cover crop on soil physical and chemical properties, for better crop nutrition

Cover crops contribute to the accumulation of organic matter in the upper layers of the soil (Roldan et al. 2003; Alvear et al. 2005; Diekow et al. 2005; Madari et al. 2005). This has been shown to result in better soil surface aggregation because of the relationship between aggregate stability and total organic carbon content in soil aggregates (Ball et al. 1996; Chenu et al. 2000; Pagliai et al. 2004). Cover crops also help promote biological soil tillage via their root development. Changes in soil structure related to root growth have been reported by several authors (Cresswell and Kirkegaard 1995). Root action can decrease soil bulk density near the surface or change pore size distribution without increasing total porosity (Henderson 1989; Rosolem et al. 2002). Whalley et al. (2005) analysed images of thin soil sections and showed the number of large pores to be greater in the rhizosphere than elsewhere because of root growth, microbial activity, and the repeated wetting and drying of the soil at the root–soil interface (Gregory 2006). Carof et al. (2007a) observed larger functional pores

and larger numbers of tubules in a no-till/cover crop system and attributed these properties to root activity. This greater biological activity in the surface layers helps increase aggregate stability and nitrogen mineralisation (Hu et al. 1995; Kiem and Kandeler 1997; Hatfield and Prueger 1996).

Cover crops have been promoted as a means of maximising the efficient use of available nitrogen in subsequent crops in agricultural systems, decreasing the risk of environmental problems associated with the nitrate contamination of surface and groundwater whilst potentially increasing profitability by reducing the need for nitrogen fertiliser (Hartwig and Ammon 2002; Wang et al. 2008). Legume cover crops can fix nitrogen, some of which is available for subsequent crops. However, the full benefit of cover crops depends on the synchronisation of cover crop nitrogen mineralisation and the nitrogen demands of the subsequent crop. Living mulches can be used to recycle nutrients and to fix nitrogen, but often compete too strongly with the main crop, decreasing crop growth and yield. Cover crop selection is therefore an important aspect of the design and optimisation of these intercropping systems (Hollander et al. 2007a, b).

4.2 Effect of a cover crop on weed communities

The principal goal of cover crops is to control weeds by replacing an unmanageable weed population with a manageable cover crop. This is accomplished by adjusting the phenology of the cover crop such that it occupies the available niches before they can be occupied by weed populations. As weeds and living mulch plants compete for the same resources, weeds can be suppressed by introducing living mulches into cropping systems (Teasdale et al. 2007). Undersown cover crops may decrease weed infestation in three ways (Phatak 1992; Bastiaans et al. 2002): preventing weed seed germination and emergence, decreasing weed growth and development, and decreasing the number of seeds present in the weed seed bank in the soil by limiting seed recruitment and increasing seed predation. The cover crop exerts its effects by rapidly occupying the open space between the rows of the main crop. Weed seed germination may be inhibited by complete light interception (Phatak 1992) by the cover crop or by the secretion of allelopathic chemicals (White et al. 1989; Inderjit and Keating 1999; Borek and Morra 2005; Hoagland et al. 2008). Allelopathy was initially defined as the effect of one plant on another through the release of biomolecules (Rice 1984). This definition was subsequently broadened to include effects on other organisms, including microorganisms in particular. Once the weed seedlings become established, competition for resources is the main mechanism of weed suppression by the cover crop (Teasdale 1998; Hollander et al. 2007b). However, it is difficult to

distinguish experimentally between allelopathy and mechanisms involving competition for growth resources. Several of the requirements for breaking dormancy and promoting weed seed germination in soils (light with a high red-to-far red ratio and high daily range of soil temperatures) are decreased more strongly by living mulches than by desiccated residues (Teasdale and Daughtry 1993). Once established, living mulches can also use the light, water and nutritional resources that would otherwise be available to weeds.

Ideally, the cover crop should suppress weed establishment during the critical period during which emerging weeds are likely to cause crop yield losses (Buhler et al. 2001). However, the major obstacle to the adoption and use of living mulches is their lack of selectivity: a living mulch that is competitive enough to suppress weeds may also decrease crop growth and yield, although this does not occur in all cases (Ateh and Doll 1996). Much of the research on living mulches has focused on developing approaches for achieving selectivity between weeds and the associated crop, including (a) sowing the living mulch so that its peak growth does not occur during the period in which competition would have the greatest impact on crop yield, (b) increasing the density of the crop population to increase the competitiveness of the crop relative to the living mulch, (c) suppressing the living mulch during crop growth so as to make it less competitive with the crop (Teasdale 1998; Teasdale et al. 2007; Hollander et al. 2007b).

4.3 Effect of a cover crop on pest communities

According to the Resource Concentration Hypothesis (Tahvanainen and Root 1972), the probability of crop pests finding their host plant is higher in monocultures of a single plant species (corresponding to the maximum concentration of the resource) than in stands consisting of a mixture of several species (in which the crop is diluted among other plant resources; Tahvanainen and Root 1972; Root 1973). This hypothesis therefore predicts a negative relationship between plant diversity and the level of invertebrate phytophagy (Root 1973) regardless of interactions with the natural enemies of pest species, constituting one of the advantages of species mixture (Malézieux et al. 2009). Many studies have tried to test this hypothesis: (a) through relationships between plant diversity and the diversity of phytophagous arthropods (Mulder et al. 1999; Koricheva et al. 2000; Haddad et al. 2001), (b) through relationships between the two extreme states (monoculture versus polyculture) and the size of phytophagous arthropod populations (Russell 1989; Andow 1991; Finch and Collier 2000), or (c) through relationships linking the density of a single plant host species and the structure of the phytoph-

agous population (Rhainds and English-Loeb 2003; Joshi et al. 2004). In contrast, few studies have investigated the effects of gradients of plant diversity on levels of phytophagy (Mulder et al. 1999; Pfisterer et al. 2003; Scherber et al. 2006; Unsicker et al. 2006). Many of these studies have been the subject of reviews (Risch et al. 1983; Andow 1986) and of a meta-analysis (Tonhasca and Byrne 1994) showing that crop diversification leads, in 52–70% of cases, to a decrease in pest density. Since the publication of these reviews, several authors have added to the debate about the consequences of crop diversification for pests (Coll and Bottrell 1995; Theunissen et al. 1995; Roininen et al. 1996; Schellhorn and Sork 1997; Harmon et al. 2003; Hooks and Johnson 2003; Aquilino et al. 2005; Costamagna and Landis 2006; Gianoli et al. 2006; Bjorkman et al. 2007; Schmidt et al. 2007). Seven of these papers reported that crop diversification successfully decreased the populations of some or all pests; four found that crop diversification had no effect, and one found that it led to an increase in the pest population. This trend suggests that the density of crop pests generally decreases in response to diversification of the plants growing on the plots. However, this trend should not be allowed to conceal the variability of the effects of crop diversification on pests or the moderate nature of these effects, even when positive.

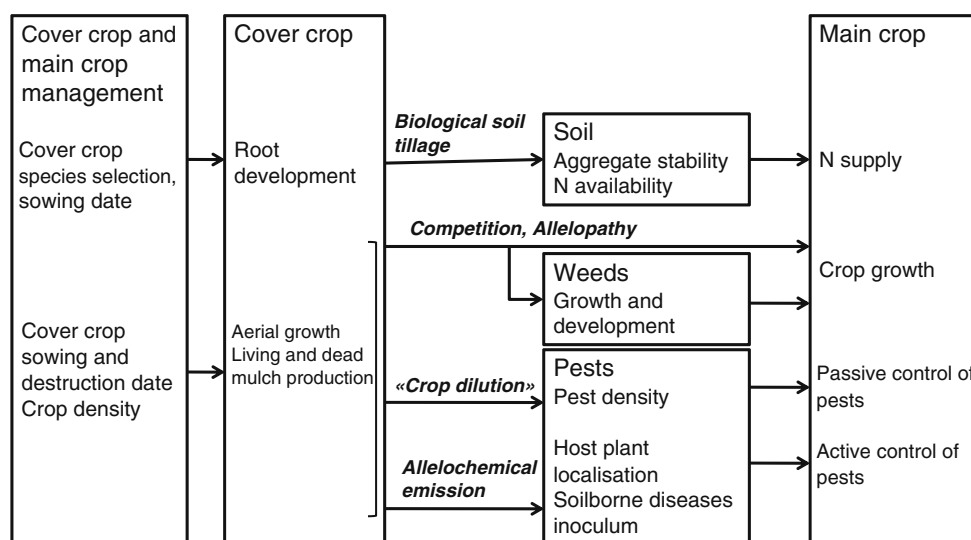
Diversifying crops to control pests, as described above, may be considered a “passive process” of control for crop-damaging organisms. Active processes may further increase the benefits of crop diversification, particularly for disease control. Such processes include changing the population of specific rhizosphere organisms, which may influence crop pathogens through competition, antagonism or suppression (Kirkegaard et al. 2008). Allelopathy is another example of an active process. The allelopathic properties of some cover crops species, such as *Brassica* crops, are increasingly viewed as an efficient way of controlling several soilborne pests and diseases. The use of these species as cover crops to control soilborne pests and diseases is called biofumigation (Angus et al. 1994). This process involves growing a *Brassica* crop (known as the break crop) during the intercrop period and then grinding it up and incorporating the residues into the soil. The direct noxious effect of allelochemicals has been clearly demonstrated in several organisms, but there is increasing evidence to suggest that other mechanisms, such as changes in the structure of soil microbial communities, may have an indirect effect on pathogens, in the long term (Yulianti et al. 2007; Mazzola et al. 2007). Motisi et al. (2009) recently observed temporal changes in the efficiency of control of the soilborne pathogen *Rhizoctonia solani* by *Brassica juncea* residues. It was suggested that the observed convex quadratic trend might result from (a) an initial decrease in efficiency due to the rapid disappearance of the allelochemicals released by

the residues and (b) a subsequent increase due to the delayed release of the remaining allelochemicals by the residues and/or a delay in the activation of microbial communities (because of the initially detrimental effect of allelochemicals) which respond to the incorporation of additional organic matter. Hence, one of the important features of biofumigation seems to be its ability to suppress soilborne diseases through biological control by antagonistic microflora organisms. Biofumigation is considered an interesting alternative to synthetic chemicals and, in principle, an environment-friendly method suitable for use in integrated pest management strategies. However, the efficiency of this technique at field scale seems to vary between studies. The implementation of this technique in current farming systems would require improvements in our understanding of the mechanisms involved in disease control, including the mechanisms by which a biofumigant crop acts on the soil environment (physical and biological components) in particular.

Many studies have shown that planting a cover crop in perennial and annual cropping systems may improve pest control (Altieri et al. 1985; Meyer et al. 1992; Wyss 1995; Pfiffner and Wyss 2004; Prasifka et al. 2006; Schmidt et al. 2007). In addition to the properties of living and dead mulches cited above (principally, the improvement of biological pest control by natural enemies, the decrease in pest damage due to crop dilution and the allelopathic effects against soilborne diseases), another mechanism has been observed. The prospecting and approach behaviour of pests is severely affected by the release of allelochemical substances from the decomposing (Mabbett 1991) or living (Finch and Collier 2000) mulch, decreasing the efficiency of crop host plant localisation. However, cover crops may also aggravate pest damage or favour new pests if the cover crop provides the pests with a key resource (Pfiffner and Wyss 2004). Indeed, pest population increases seem to occur more frequently with living than with dead mulches (Meyer et al. 1992; Costello and Altieri 1995).

Figure 3 illustrates the beneficial effects of cover crops described above. The introduction of a cover crop increases the diversity of the plants growing on the field. Previous studies have shown that this diversification, by modifying biotic and abiotic components, provides important services, such as capturing soil nutrients and preventing their loss, nitrogen fixation by legumes, increasing soil carbon levels and associated improvements in soil physical and chemical characteristics, increasing biological activity and diversity and suppressing weeds and pests (Lal et al. 1991; Hartwig and Ammon 2002). These services can improve resource availability and the growth conditions of the crop or decrease the impact of pests, thereby increasing crop productivity. Nevertheless, the introduction of a cover crop may also decrease resource availability (competition with

Fig. 3 Main effects of the introduction of a cover crop on biotic interactions and agricultural practices for managing these effects



the main crop for light, nutrients and water) or favour new pests and diseases, thereby decreasing crop productivity (Teasdale et al. 2007; Carof et al. 2007b; Shili-Touzi et al. 2009). In this review, we show that the trade-off between the services and deleterious effects resulting from the introduction of a cover crop can be managed through agricultural practices (choice of the cover crop species, sowing and destruction dates, etc.), but the reported efficiency of these techniques differs between studies. The main reason for this variability is the sensitivity of biotic interactions to environmental conditions at the field scale (Altieri et al. 1985). The use of this technique in current farming systems therefore requires improvements in our understanding of the mechanisms involved, making it possible to identify indicators and rules for determining the best trade-off, taking into account the local environmental conditions, the means of the farmer and production objectives.

5 Taking into account the non-crop habitats in rural landscapes

Modern agricultural landscapes generally vary from extremely simple structures, which mainly consist of arable fields, to highly complex landscapes, comprising interconnected semi-natural habitats. Due to a range of farming practices, such as soil tillage, sowing, pesticide applications, mineral fertilisation or harvest, arable fields may be seen as relatively ephemeral habitats subject to frequent disturbances. Semi-natural habitats, or non-crop habitats—such as hedgerows, field margins, fallow land or woodlots—are less prone to perturbation than annual crops and thus provide more stable habitats. The main reason for taking large scales into account in biotic interactions is that many species (pests, and natural enemies, diseases) live and reproduce within these two types

of habitat. It is therefore important to understand how these landscape features influence biotic interactions. In this section, we will first describe the role of these non-crop areas. We will then identify the relevant landscape characteristics for biotic interactions and, finally, discuss the practical impact in terms of biological control.

5.1 The effects of non-crop habitats on pests, their natural enemies and diseases

Crop habitats are often considered to be detrimental for many animal species, including the natural enemies of phytophagous insects (Bianchi et al. 2006), whereas non-crop habitats are thought to favour beneficial species directly or indirectly by providing important life support functions. Non-crop habitats have been found to affect arthropod populations directly by providing them with shelter. Indeed, several studies have shown that herbaceous vegetation and woody habitats provide a more moderate microclimate than crop fields, protecting natural enemies against temperature variations (Rahim et al. 1991). Dyer and Landis (1996) comparing the longevity of the parasitoid *Eriborus terebrans* in maize fields and various non-field habitats, found greater longevity in woodlots than in maize fields. It has been shown that the levels of parasitism of insect pests are higher close to the edges of fields bordering non-crop habitats than in the centre of fields due to a moderately mild microclimate and the availability of nectar (Altieri and Schmidt 1986; Landis and Haas 1992; Thies and Tscharncke 1999). Non-crop areas are also known to provide natural enemies and pests with adequate overwintering habitats, increasing winter survival and thus favouring crop colonisation in the spring.

Non-crop areas may also influence natural enemy populations by supplying food resources for many insects (Bugg and Pickett 1998). In particular, predators and

parasitoids are thought to make use of sugar-rich materials derived from plants, such as nectar, pollen or honeydew, to cover their energy requirements (Jervis et al. 1993; Wäckers et al. 2005). Several studies have demonstrated that more diverse vegetation, including flowering weeds, results in a greater availability of pollen and nectar, leading to higher densities of predators, such as carabid beetles and syrphid flies (Lys et al. 1994; Hausammann 1996; Sutherland et al. 2001). Experimental studies have also demonstrated that nectar feeding increases the survival and fecundity of various natural enemies of pests (Winkler et al. 2006, 2009; Tompkins et al. 2010). Many hymenopteran parasitoid species have been found to feed on floral nectar (Jervis et al. 1993; Wäckers 2001), with higher levels of nectar availability associated with higher rates of parasitism (Berndt et al. 2006; Ellis et al. 2005; Stephens et al. 1998). More generally, the presence of floral resources in semi-natural habitats has been found to affect the diversity, distribution and abundance of parasitoids (Marino et al. 2006). Semi-natural habitats may also increase food resources in the form of alternative hosts and prey (Landis et al. 2000; Denys and Tscharrnke 2002; Thomas 2002). This enhances biological pest control by providing additional hosts and prey at times when these species are present at low density in fields, thereby increasing the fitness of natural enemies of pests. For example, Corbett and Rosenheim (1996) found that the presence of semi-natural habitats supporting alternative hosts significantly increased the density of the egg parasite *Anagrus epos* at the field and landscape levels.

Few studies have investigated the effects of non-crop habitats on diseases caused by fungi and bacteria. As a result, the role of landscape effects in disease epidemiology remains largely unknown for most crop diseases (Plantegenest et al. 2007), apart from those in which the pathogen's life cycle includes two different host species. For example, the barberry (*Berberis vulgaris*) eradication programme has successfully improved wheat stem rust control (Campbell and Long 2001).

5.2 Relevant landscape characteristics for biotic interactions

As shown by the examples above, non-crop habitats may play different roles at different periods in the year (e.g. overwintering habitat, source of alternative prey, pollen or nectar) and organisms can move between crop and non-crop habitats. All the ecological functions provided by these non-crop areas affect population dynamics. Landscape ecology has described a framework for understanding the ecological processes operating in a landscape (Dunning et al. 1992). The authors identified four types of processes: landscape complementation, landscape supplementation,

source/sink dynamics, and neighbourhood effects. We summarise here the main hypothesis connecting landscape patterns and population dynamics.

Landscape complementation occurs when a species requires different non-substitutable resources in its life cycle. The presence of a resource in one habitat is complemented by the presence of another resource in a nearby habitat, resulting in larger populations being supported in the vicinity of these habitats. The organism must travel between two different resources at some point in its life cycle. This process is particularly well illustrated by species requiring specific winter habitats, such as pests of winter oilseed rape: pollen beetle, cabbage seed pod weevil (Ulmer and Dodsall 2006b; Alford et al. 2003). The landscape supplementation hypothesis states that the population of a patch may be higher if that patch is located close to other patches of the same resource. In this process, resources within the landscape are substitutable, increasing their accessibility. Source/sink relationships occur when habitats serve as sources of emigrants, which disperse to less productive habitats called sinks. Subpopulations in the patches of sink habitat would become extinct without this immigration. Finally, neighbourhood effects occur when a species is more strongly influenced by the characteristics of contiguous patches than by those of patches located further away.

These types of processes have been illustrated in recent studies highlighting the crucial role of the interface between crop and semi-natural areas in population dynamics. Important resources available in non-crop areas allow beneficial arthropod populations to increase in size and to spill over into crop fields (Tscharrnke et al. 2007). Indeed, several studies have demonstrated that semi-natural habitat patches adjacent to arable fields affect top-down control (Bianchi and Wäckers 2008; Olson and Wäckers 2007). However, Rand et al. (2006) demonstrated that the direction of spillover effects is determined principally by the primary productivity of habitats, and spillover may therefore occur from crop areas towards non-crop habitats. Indeed, arable fields represent high-resource habitats for populations of the natural enemies of pests during part of the year, allowing beneficial arthropod populations to increase in size and then to migrate to less productive areas by passive diffusion. The brutal destruction of the habitat due to harvesting leads to the active emigration of predators from the cultivated habitats towards more stable semi-natural habitats. Thus, most natural enemies rely on the resources provided by semi-natural environments (according to Keller and Häni 2000, with nine in every ten beneficial species requiring non-crop environments at some point in their life cycle, whereas this is the case for only one in two pest species), and some regularly travel between these habitats and the crop. This is observed particularly in highly

fragmented European landscapes in which the presence of beneficial species in crops increasingly depends on the regular arrival of individuals from semi-natural habitats to recolonise the plot (Schmidt et al. 2005). Thus, both landscape composition (the proportion of non-crop habitats) and configuration (the spatial location of these habitats) are important factors influencing the dynamics of insect pest and natural enemy populations.

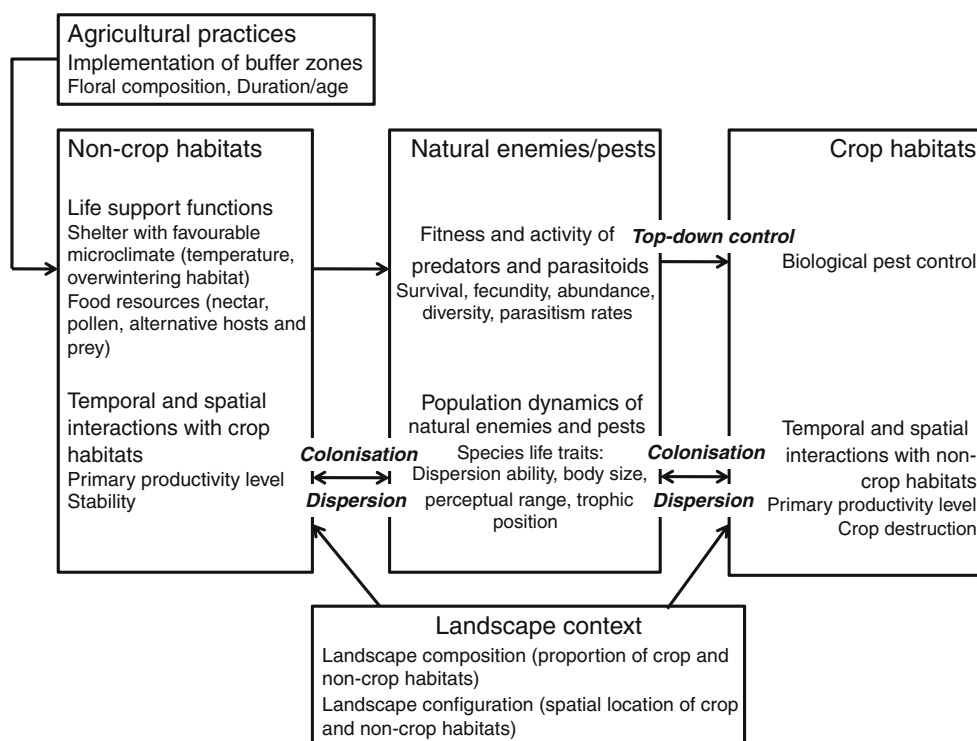
Similarly for diseases, it has been predicted that not only the proportion of the landscape occupied by the host crop but also the spatial configuration of field plots (size and distance between plots of host crops, in interaction with dispersal distance) should affect the dynamics of plant disease epidemics (Gubbins et al. 2000). Diseases spreading within and between agricultural fields in a landscape can be studied within a metapopulation framework (Gilligan 2002). Theoretically, it is possible to predict the probability of colonisation and disease extinction in individual subpopulations (e.g. fields) and at the landscape scale as a function of disease transmission (within and between subpopulations), host replacement or removal rates and the number and size of subpopulations (Park et al. 2001). This theory has been tested in natural and semi-natural habitats, with wild plant patches as subpopulations (Burdon et al. 1995; Ericson et al. 1999), but it has yet to be tested in agricultural systems, with fields as subpopulations (Gilligan 2008).

For determination of the level at which pest management strategies should be implemented, it is necessary to identify the scale at which species respond to landscape context. Species life history traits, such as the ability to disperse, body size, perceptual range and trophic position, are assumed to be key elements of the reaction of populations to spatial context (Tscharntke et al. 2007). Species of higher trophic levels are generally considered to experience the landscape at larger spatial scales and to be less affected by local habitat quality than species of lower trophic levels (Tscharntke et al. 2007). According to Tscharntke et al. (2005), this appears to be true only if there is a positive correlation between trophic level and body size. Natural enemies of the same trophic level may operate at different spatial scales due to their dispersal abilities and specialisation. For example, generalist predators respond to larger spatial scale than specialist predators (Tscharntke et al. 2005). To make matters worse, the ability to disperse is not a species-specific fixed trait, but more an individual trait that can display variation within and between populations of the same species and be affected by the configuration of the landscape itself because landscape context exerts selective pressure on dispersal ability (Baguette and van Dyck 2007). Thus, the spatial arrangement of crop and non-crop habitats in the landscape affects both dispersal and colonisation abilities.

5.3 Practical implications

One of the main ways in which non-crop habitat effects can be used for pest control is through the implementation of buffer zones (hedgerows, beetle banks, adjacent field margins, field boundaries, conservation strips). Indeed, it is now known that the lack of adequate food in agricultural landscapes is one of the major factors limiting populations of beneficial insects (Wäckers et al. 2005). Several insect species consume nectar and pollen to provide energy for maintenance and fecundity, so the provision of food supplements is one approach to increasing the sizes of populations of beneficial species (Colignon et al. 2004; Rebek et al. 2006). Many studies have been carried out in English- and German-speaking countries on single-species flowering strips (e.g. White et al. 1995; Hickman and Wratten 1996; Petanidou 2003; Pontin et al. 2006) and flower strips composed of several species (Sutherland et al. 2001; Scarratt et al. 2004; Rebek et al. 2005; Luka et al. 2006; Pontin et al. 2006) and their effects on flower-dependent specialist predators and parasitoids. It has often been reported that the effects of these strips on the biodiversity of beneficial species depend heavily on the types of plant present. In Switzerland, major studies have been carried out since the start of the 1990s to determine the species composition of flower strips most favourable for all sorts of beneficial zoophagous species (Nentwig 1992, 1998; Nentwig et al. 1998; Wäckers 2004). Field margins with a naturally diverse flora harbour the greatest abundance and diversity of arthropods (Lagerlöf and Wallin 1993). In a recent study, Carvell et al. (2007) compared the efficacy of various field margins for enhancing the diversity and abundance of bumblebees. They found that uncultivated margins sown with mixtures containing nectar- and pollen-producing plants were more effective at providing bumblebee forage than margins sown with a grass mixture. Many studies have shown that the effects of these buffer zones depend strongly on their age. Flower strips favouring the development of flower-dependent specialist predators and parasitoids also make very good refuges for ground-dwelling beneficial species 2–3 years after the planting of several tussock grasses (Nentwig 1988; Frank and Nentwig 1995; Pfiffner and Luka 2000; Meek et al. 2002; Frank et al. 2007). Beetle banks appear to retain a dense vegetation structure, with a high species richness and diversity, 3 years after implementation and over a period of more than 10 years (Thomas et al. 2002). Field margins or conservation strips harbour natural enemies of pollen beetles if they are more than 6 years old, as observed by Büchi (2002) and Thies and Tscharntke (1999). These results are also confirmed by the significant differences in parasitism rates and pollen beetle damage observed in 6-year-old field margins (Thies et al. 2003).

Fig. 4 Principle biotic interactions between non-crop and crop habitats and impacts of agricultural practices and landscape context



There is growing evidence that complex landscapes are often associated with a greater diversity of natural enemies, but few studies have dealt with the real impact of this biodiversity on pest control. Bianchi et al. (2006) reviewed numerous studies concerning the effect of landscape complexity on pest and natural enemy populations. They found that more complex landscapes with high proportions of semi-natural habitats were associated with higher levels of natural enemy populations than simple landscapes in 74% of studies and with lower levels of pest damage in 45% of studies. They suggested that the effects of increasing landscape complexity on various natural enemies ranged from an increase in oviposition rates by a factor of 1.6 to an increase in parasitism rates by a factor of 10. However, only ten studies considered the consequences for pest pressure. In 45% of these studies, pest pressure was found to be lower in structurally complex landscapes: lower aphid densities, thrips densities, and fewer symptoms and lower levels of crop damage caused by pollen beetle were reported. Moreover, landscape complexity did not affect pest pressure in 40% of the studies, in some cases due to a higher rate of pest establishment associated with higher rates of pest mortality inflicted by natural enemies. Recent studies on the diversity of natural enemies have often concluded that increasing the species richness of predators results in the more efficient suppression of herbivorous pests (Snyder et al. 2006; Cardinale et al. 2003).

All recent studies of population dynamics and trophic interactions at the landscape scale have provided strong

evidence that biotic interactions should be considered at a larger scale than a single patch of habitats. Figure 4 shows the main ways in which these landscape effects act. Nevertheless, three types of difficulties have been identified:

1. In most landscape-scale studies, pest damage and effective biotic interactions are not taken into account, resulting in gaps in our knowledge about the real effects of non-crop habitats on pest control and yield losses. As a result, although the role of large-scale processes has been highlighted, it remains unclear how best to make use of landscape effects and to implement integrated pest management strategies at this scale.
2. For the implementation of efficient integrated pest management schemes involving a reconfiguration of the landscape, it is of crucial importance to know the scale at which species respond to landscape pattern. This is particularly difficult to determine as this scale may differ between species, and even between populations of the same species.
3. Landscape-scale studies have mostly neglected the diversity of farming practices that may affect population dynamics at the field scale and/or dispersal ability. Thus, a more precise description of crop management and cropping systems at the landscape scale may highlight ways to maximise biotic interactions.

The complexity of biotic interactions within the agroecosystem (multiple trophic levels, acting at multiple

spatial scales and affected by multiple farmers' decisions) suggests that the modelling of ecological processes at rural landscape scale may be necessary to determine whether or not it is possible to regulate pests in this way within the rural landscape and how to optimise this management. Much remains to be done to elucidate the processes acting at the landscape scale, to transform this knowledge into quantitative relationships and to design a new spatial organisation of crops, cropping practices and non-crop habitats enhancing the biological control of pests and diseases.

6 Discussion

From this review, we can conclude that each of the four approaches described is suitable for the management of agroecosystems to enhance biotic interactions. Each of these approaches can also be seen as a level at which decisions can be taken by the farmers (decision rules for a single technique, crop management, crop sequence, landscape management) and as providing several degrees of freedom within biological processes for the reorientation of these processes towards favourable biotic interactions, at least in terms of crop protection and nutrition. Modifications affecting plant diversity in particular seem to enhance biotic interactions particularly effectively. Plant diversity, which must be considered at several levels (crop in mono- or pluri-species plant populations, weeds, plants from non-crop habitats), plays a fundamental role in biotic interactions. Plants form the first level of the food web, supporting both pests and natural enemies, which they can then control (bottom-up regulation: Gurr et al. 2003; Swift et al. 2004). They also affect the habitats for other taxa from field (through biological soil tillage and cover crops) to landscape scale (hibernation shelter for natural enemies).

This review is not exhaustive, focusing on a few typical examples for each approach. However, it nonetheless demonstrates that for both crop protection and crop nutrition, biological processes constitute a wonderful source of tools on which agronomists and farmers can act. Most of these tools were unknown to science before the first steps towards the modernisation of agriculture were taken, half a century ago. However, farmers have nevertheless empirically made use of some of these tools, embedding them in agronomic rules (crop rotations, traditional fertilisation decision rules, etc.). It is not possible to face the current challenges of agriculture by simply reverting to these traditional rules, which applied to a different environment (e.g. the main pest species were not the same) and gave yields much lower than those required today. The handling of biotic interactions is thus both an opportunity and a necessity.

Although there seems to be an almost infinite range of ecological processes at our disposal, this review shows that we remain far from fulfilling our aims. Several limitations have been identified for some of the approaches considered. First, qualitative data often exist, but we still lack precise and quantitative reference data concerning the consequences of technical changes for biotic interactions. This is mostly due to the complexity of the responses of agroecosystems to management systems. For example, the introduction of a new cover crop may affect agroecosystems in several ways. Cover crops may interact with weeds by both allelopathy and competition. This makes it difficult to decorrelate processes to evaluate their individual impacts on crop production. As the scale of study increases, these confounding effects may increase, involving more temporal and spatial interactions. Studies at the landscape scale provide us with insight into the ecological significance of landscape composition and spatial organisation, making it possible to understand how pest or disease control could be strengthened. However, the role of landscape characteristics in the biocontrol of pests remains a matter of debate (e.g. Bianchi et al. 2006 for insect pests) because increasing the natural enemy population in crops does not necessarily guarantee effective pest control, and the relationships between crop and non-crop habitats are complex and sometimes antagonistic (Thies and Tschardt 1999; Valantin-Morison et al. 2007). Further studies are therefore required to quantify the effects of landscape composition and spatial organisation not only on natural enemies but also on pest pressure and pest damage. Furthermore, the impact of crop management changes is often limited, and such changes may have opposite effects. For example, mulches may increase the populations of both pests and their natural enemies. A hierarchy of potential pests should be generated as a function of what is known about the history of the field and the surrounding area. This is necessary because one pest population may benefit from techniques designed to limit another. Moreover, some of the studies covered by this review highlight the variability of the responses observed in terms of biotic interactions: beneficial, negative or neutral effects. This variability may make it difficult to establish general trends for a given biotic interaction in different agroecosystems and pedoclimatic conditions.

Second, another obvious limitation of most studies is that they do not consider the goals and constraints of the farmers (at the farm level) and other stakeholders (at the landscape level). Some of the most promising decision rules, even if supported by strong quantitative data, may remain completely ineffective if they conflict with more important issues.

Third, the effects of cropping techniques are often considered separately, although agronomists are well aware

that the effects of a given technique should not be considered in isolation because, as in any complex system, there may be interactions between techniques or between techniques and the environment. The relationship between sowing date and the severity of phoma stem canker on oilseed at the end of the crop cycle is a good example because it is not straightforward and is well documented. Early sowing dates have been reported to limit the severity of phoma stem canker in England (Gladders and Musa 1980) and in Western Australia (Khangura and Barbetti 2001). However, late sowing dates have been reported to generate less severe phoma stem canker in Australia (MacGee and Emmett 1977) and in Europe (in Germany and the Netherlands: Scheibert-Bohm 1979; in France: Lepage and Penaud 1995). In addition, several studies in Canada have reported a lack of effect of sowing date on phoma stem canker severity because the inoculum is released throughout the growing season (Kharbanda and Tewari 1996). Finally, very early sowing (about 1 month before the usual date) did not affect the severity of phoma stem canker in 36 of 49 trials carried out over a 3-year period in France (Dejoux et al. 2003). Some crops sown very early even had more severe phoma stem cankers than crops with a typical sowing date, in 10 of the 49 trials. This finding may be due to the existence of considerable variability in the dynamics of primary inoculum production (Salam et al. 2007), and for a given sowing date, crop emergence and early seedling development may also be delayed by unfavourable conditions (e.g. drought). For this reason, Aubertot et al. (2004) concluded that synchronisation between primary inoculum production and susceptible stages of oilseed rape (from the cotyledon stage to the six-leaf stage) was responsible for severe canker rather than that early sowing date systematically led to more severe phoma stem canker. Similar interactions have been reported for other pests. For instance, Dejoux et al. (1999) showed that advancing the sowing date of oilseed rape by 15 days controlled weeds only if soil nitrogen levels were sufficiently high. Furthermore, in some cases, the effect of sowing date on synchronisation with the life cycle of pests may be antagonistic for different organisms. Indeed, Valantin-Morison et al. (2007) showed that early sowing of winter oilseed rape tended to increase root maggot (*D. radicum*) damage, whereas it was associated with a lower level of attack by cabbage stem flea beetle (*Psylliodes chrysocephala* (L.)). Moreover, interactions may exist not only within a level but also between levels. For example, landscape composition was the only factor taken into account in most of the studies we analysed, although the different cropping systems in farmland and the various types of crop management (e.g. distribution of resistant varieties, ploughed area, or frequency of pesticide utilisation) in the

landscape should be considered in analyses of the impact of agriculture on metapopulations.

In this review, we focus on two ecological services provided by biotic interactions: non-chemical crop protection and improvements in crop nutrition. The benefits and limitations identified define a clear research agenda, which can probably also be adapted to other services (such as primary production or pollination). The first step is to complete our understanding of the responses of biotic interactions to management. For this purpose, we must identify the processes involved and the relevant cropping operations as a function of both the organisms and interactions considered. For instance, pest management may concern all levels of the cropping system, whereas the improvement of crop growth conditions is related to operations at the field scale, including the field margin. This agroecological research should focus on systemic approaches taking into account interactions and quantitative approaches. Several approaches could be useful to explore the variability of responses: meta-analyses, modelling and experiments on multiple sites, similar to those carried out in ecology (e.g. international experimental design for the study of diversity and functional relationships in grasslands; Spehn et al. 2005). The second step is to design agroecosystems based on this knowledge. The opposite effects of the conflicting processes these systems entail must be taken into account, but are all too often neglected. In addition to field and farm experiments, modelling approaches have been developed for the *ex ante* assessment of agroecosystem sustainability (Sadok et al. 2009).

7 Conclusion

It seems possible to manage biotic interactions in agroecosystems in several ways by modifying single practices, such as cultivar choice, or entire landscapes. The limiting factor does not seem to be the ecological processes, but our ability to quantify their response to management by humans and to valorise them, taking into account the multiple interactions occurring between processes and levels of management. Handling biotic interactions through the complex assembly of agricultural techniques at various temporal and spatial scales seems to be a highly promising but still largely unexplored avenue.

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