CHAPTER SIX

BIOLOGICAL CONTROL OF INSECT PESTS IN AGROECOSYSTEMS: EFFECTS OF CROP MANAGEMENT, FARMING SYSTEMS, AND SEMINATURAL HABITATS AT THE LANDSCAPE SCALE: A REVIEW

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Abstract

There is a growing body of evidence to suggest that the simplification of land uses associated with a strong dependence on agrochemical inputs is decreasing environmental quality, threatening biodiversity, and increasing the likelihood of pest outbreaks. The development of farming systems with greater reliance on ecosystem services, such as biological control of insect pests, should increase the sustainability of agroecosystems. However, the factors responsible for the maintenance or enhancement of natural pest control remain unclear. The goal of this review is, therefore, to expose which elements, from the field to the landscape scale, influence natural enemy populations and pest regulation. We present here the principal effects of seminatural habitats, farming systems, and crop management on the abundance of insect pests and their biological control, with a view to evaluating their relative importance and identifying key elements that regulate natural pest control interactions. Because of the range of spatial and temporal scales experienced by these organisms, we advocate, in studies investigating trophic relations and biological pest control, a clear description of cropping systems and an explicit consideration of seminatural habitats and more generally of the surrounding landscape. Through this review, we also indicate gaps in knowledge and demonstrate the interest of linking agronomy and landscape ecology to understand trophic interactions, maximize natural pest control, and limit pesticide applications. Quantifying the relative importance of both local and landscape scales is a fundamental step in the design and assessment of ecologically sound integrated pest management strategies for farmers.

1. INTRODUCTION

Modern agricultural landscapes are generally characterized by a high proportion of arable fields, large field sizes, and a high degree of fragmentation of seminatural habitats into small units (Baessler and Klotz, 2006; Tscharntke *et al.*, 2005). There is also a growing body of evidence to suggest that the simplification of land uses associated with a strong dependence on agrochemical inputs is decreasing environmental quality and threatening biodiversity (Evenson and Gollin, 2003; Millennium Ecosystem Assessment, 2005).

There is, therefore, a need to reduce pesticide use by developing innovative cropping systems to ensure the sustainability of agricultural production.

Biodiversity conservation and the development of farming systems with greater reliance on ecosystem services should together increase the sustainability of agroecosystems and landscapes (Altieri, 1999; Hillel and Rosenzweig, 2005). Ecosystem services include production, nutrient cycling, flood regulation, climate regulation, biological control of pests, and aesthetic value (Costanza *et al.*, 1997; Millennium Ecosystem Assessment, 2005; Zhang *et al.*, 2007). The sustainability of an agroecosystem depends on various ecosystem services, but may also be affected by ecosystem disservices, such as herbivory, which decrease productivity and increase production costs (Zhang *et al.*, 2007). For these reasons, natural pest regulation is considered one of the most important services of biodiversity (Fiedler *et al.*, 2008; Schläpfer and Schmid, 1999; Wilby and Thomas, 2002), with an estimated value of more than 400 billion dollars (US) per year worldwide (Costanza *et al.*, 1997). The generalized intensification of agriculture and the use of broad-spectrum pesticides decrease the diversity of natural enemy populations (Basedow, 1990; Koss *et al.*, 2005) and increase the likelihood of pest outbreaks (Lawton and Brown, 1993; Swift *et al.*, 1996). Indeed, pesticide use has been shown to be associated with a large decrease in natural pest control services (Cross *et al.*, 1999; Prokopy *et al.*, 1995). Thus, enhancement of the natural regulation functions of agroecosystems appears to be one of the main ways in which we can decrease the use (Wilby and Thomas, 2002) of chemical pesticides for pest control and increase the sustainability of crop production. However, the factors responsible for the maintenance or enhancement of natural pest control remain unclear. Moreover, the environmental and economic benefits to farmers of increasing the activity of natural enemies of crop pests remain a matter of debate, in the absence of clear scientific evidence.

Recent reviews have shown that biological control depends on multiple levels ranging from field to landscape scales (Gurr *et al.*, 2003; Tscharntke *et al.*, 2007). It has been shown that community structure, species richness and abundance, and population dynamics and interactions within and between trophic levels are affected by spatial context (e.g., patch size, spatial configuration, landscape composition, habitat connectivity, or even the structural complexity of habitats) (Bianchi *et al.*, 2006; Finke and Denno, 2006; Kareiva, 1987; Marino and Landis, 1996; Tscharntke and Brandl, 2004; Woodcock *et al.*, 2007; Zabel and Tscharntke, 1998). Crop management and farming systems have also been shown to have major effects on species composition, abundance, and distribution in agroecosystems (Bengtsson *et al.*, 2005; Booij and Noorlander, 1992; Cárcamo, 1995). However, the relative contributions of crop management, farming systems, and landscape context to pest abundance, natural enemy abundance, and biological control have been poorly studied (but see Roschewitz *et al.*, 2005b).

We review here the principal effects of landscape context, farming systems, and crop management on the abundance of insect pests and their biological control, with a view to evaluating their relative importance and identifying key elements that regulate natural pest control interactions. We consider here a system with three trophic levels as a general framework, taking host–parasitoid interactions as a particular example, with the aim of providing a complete overview of all the mechanisms and interactions involved in biological control processes. We will begin by exploring the factors driving arthropod dynamics at the landscape scale. We will then move on to the role of seminatural habitats for pest and natural enemy populations and present a concise overview of the main effects of landscape context on natural pest control. We will then present the state of the art on the relationships between natural enemy biodiversity and pest suppression. Thereafter, we will report the effects of various crop management elements at a local scale (i.e., habitat scale) on pest and natural enemy populations. The effects of farming systems on trophic interactions will then be assessed, with the aim of identifying biological control mechanisms at the farm level. This will lead on to the conclusion, in which we will highlight the value of considering the combined effects of landscape, farming systems, and crop management on biological control interactions, focusing particularly on the effects of crop management, which are frequently neglected. Throughout this review, we will highlight the importance of the precise description of crop areas, crop management, and seminatural habitats in studies of trophic interactions and discuss the direct benefits of such approaches for integrated pest management strategies.

2. ARTHROPOD DYNAMICS AND TROPHIC INTERACTIONS WITHIN THE AGRICULTURAL LANDSCAPE

Large-scale approaches are required for studies of population dynamics and community ecology (Tscharntke and Brandl, 2004; Tscharntke *et al.*, 2007). The need for a large-scale perspective in studies of predator–prey interactions was first highlighted in spatial ecology studies, principally through theoretical and empirical works on the structure and dynamics of fragmented populations (Cronin and Reeve, 2005). In particular, works on metapopulations have increased our theoretical understanding of the dynamics of insect pests and their natural enemies in fragmented landscapes (Hanski and Gaggiotti, 2004; Levins, 1969). In metapopulation theory, the regional persistence of a population is made possible by a stochastic balance between the extinction of local populations and the colonization of previously empty habitat patches (Levins, 1969). It has been suggested that habitat fragmentation and dispersal ability are the driving forces behind the regional persistence of host–parasitoid populations (Hanski and Gilpin, 1997; Hassell *et al.*, 1991). The population dynamics of such systems are highly variable and depend on species characteristics and landscape organization (Tscharntke and Brandl, 2004).

According to Hanski and Gilpin (1997), a population functions as a metapopulation when its hosts are distributed in discrete patches, local populations on patches have a high probability of extinction, unoccupied patches are available for colonization, and local subpopulations do not fluctuate asynchronously. As reported by Elliott *et al.* (2008), the first three of these criteria are usually satisfied for most insect pest populations, but the fourth criterion remains uncertain, because climatic factors generally have a major influence on insect pest dynamics. In the case of host–parasitoid interactions, the small body size, high rate of population increase, and specialization are thought to predispose them to metapopulation dynamics (Cronin and Reeve, 2005). However, experimental evidences for key factors that drive host–parasitoid metapopulation are rare. In their review, Cronin and Reeve (2004) described several experimental studies, in which the spatial population structure of eight different hosts and their parasitoids have been characterized. They demonstrated that (i) the population structures of different host–parasitoid systems are highly variable, (ii) the parasitoid and its host generally respond to spatial subdivision at different spatial scales, (iii) parasitoids can cause the local extinction of host populations, and (iv) parasitoids are usually more prone to extinction than their host.

Spatial ecology studies have identified diverse responses of populations to habitat loss and fragmentation. A classical metapopulation (*sensu* Levins, 1969) is one of several spatial population structures that may emerge. Others include mainland-island metapopulations (Pulliam, 1988), ephemeral aggregations of individuals, isolated populations, and synchronized local populations (Hirzel *et al.*, 2007). Hirzel *et al.* (2007) showed, by modeling, that five classes of spatio-temporal dynamics could be distinguished (i.e., metapopulation, mainland-island, spiral fragments, spatial chaos, and spirals) for host–parasitoid systems with varying three parameters: proportion of suitable habitat, spatial autocorrelation, and host dispersal rate. This study confirmed that dispersal rate and landscape configuration are major factors influencing local extinction and colonization events, highlighting the importance to take the landscape-scale and species-specific traits into account to understand population dynamics and trophic interactions.

While the first approach (the metapopulation approach) is based on a strong theoretical background and on mathematical models to predict the responses of species to spatial context, a second more empirical approach came from landscape ecology. Whereas the metapopulation approach considers the matrix to be an unsuitable habitat, the landscape ecology approach considers different classes of patches in the surrounding landscape according to their functional role on population dynamics between and within patches. Dunning *et al.* (1992) described the principal processes affecting populations in landscape-based approaches. Four classes of ecological processes with important effects on local populations have been identified: landscape complementation, landscape supplementation, source/sink dynamics, and neighborhood effects. Landscape complementation occurs in situations in which a species requires at least two different nonsubstitutable resources at particular points in its life cycle. These resources may be foraging patches, breeding sites, or overwintering sites. The presence of a resource in one type of patch is complemented by the presence of the other type of resource nearby in another type of patch, making it possible to support larger populations in the proximity of these patches. According to the landscape supplementation hypothesis, as described by Dunning *et al.* (1992), the population of the focal patch may be enhanced if that patch is located close to other patches of the same resource or patches that have the same function. In this process, resources within the landscape are substitutable, increasing their accessibility. Source/sink relationships appear when productive patches serve as sources of emigrants, which disperse to less productive patches. Local populations in sink patches cannot be maintained without this immigration. Finally, neighborhood effects exist when the species abundance in a particular patch is more strongly affected by the characteristics of contiguous patches than by those of patches located further away. These four ecological processes have been demonstrated for various species, by empirical studies at the landscape scale (Dunning *et al.*, 1992; Frouz and Kindlmann, 2001; Haynes *et al.*, 2007; Ouin *et al.*, 2004). The general framework proposed by Dunning *et al.* (1992) links general landscape pattern (structural composition of the landscape) to the habitat-specific responses of organisms (Kareiva, 1990) and the ecological processes of population dynamics. Both the metapopulation and landscape ecology approaches, with their differences and limitations, suggest that a landscape-wide perspective is required if we are to understand the dynamics and interactions between local populations.

Communities consist of species influenced by different spatial and temporal scales due to species-specific life-history traits, such as the ability to disperse, body size, competition and sensitivity to disturbance, microhabitat specialization, or trophic position. Parasitoid and their hosts, for example, generally react differently to spatial contexts (Cronin and Reeve, 2005; Ryall and Fahrig, 2005; With *et al.*, 1999). Classically, species at higher trophic levels are thought to operate at larger spatial scales and to be less affected by local patch quality, because they tend to disperse to a greater extent (Holt, 1996). However, Tscharntke *et al.* (2005) found this to be the case only if there is a positive relationship between trophic level and body size (and thus, dispersal abilities). Indeed, predators of the same trophic level may experience the surrounding landscape at different spatial scales, depending on their abilities to disperse and specialization, with generalist predators operating at a larger scale than specialist predators (Tscharntke *et al.*, 2005). However, a species operating at a low trophic level, but with a large capacity for active or passive dispersal, may experience the surrounding landscape at a larger scale than a species operating at a higher trophic level, but with poorer dispersal. For example, Roschewitz *et al.* (2005b) showed that the abundance of cereal aphids at wheat ripening was significantly influenced by landscape complexity at all five spatial scales (from 1 to 3 km) explored in their study, whereas the parasitoids of these aphids responded to landscape complexity at three spatial scales from 1 to 2 km. Moreover, several studies have shown that habitat fragmentation often affects the abundance and diversity of predators and parasitoids more strongly than those of their herbivorous hosts (Kruess and Tscharntke, 1994; Zabel and Tscharntke, 1998). Indeed, species operating at higher trophic levels may be more prone to extinction than those at lower trophic levels, because of their lower densities, more variable population size, narrower and more fragmented distribution of resources, dependence on the successful colonization of patches by hosts of lower trophic levels, and sometimes smaller capacity for dispersal (Davies *et al.*, 2000; Holt, 1996; Kruess and Tscharntke, 1994; Purvis *et al.*, 2000; Thies *et al.*, 2003). Thus, the control of prey and host species by their specialist natural enemies may be disrupted by increasing seminatural habitat fragmentation. As the scale-dependency differs between species and is determined, in particular, by the ability of different species to disperse, local habitat effects may play a major role in population dynamics of species dispersing over short distances, whereas generalist predators are influenced by landscape context at large spatial scales.

3. THE ROLE OF SEMINATURAL HABITATS ON PEST AND NATURAL ENEMY POPULATIONS

Seminatural habitats, such as forests, hedgerows, field margins, fallows, and meadows support a large number of pest and natural enemy species, as they provide a more stable environment than annual crops. Generally, these habitats house a larger proportion of neutral and beneficial arthropods than detrimental arthropods (Denys and Tscharntke, 2002; Marshall, 2004; Thomas *et al.*, 2002). Indeed, such habitats provide life support functions, maintaining populations of alternative hosts and prey for predators and parasitoids (Fig. 1) (Denys and Tscharntke, 2002; Kozar *et al.*, 1994; Pickett *et al.*, 2000; Sotherton, 1984).

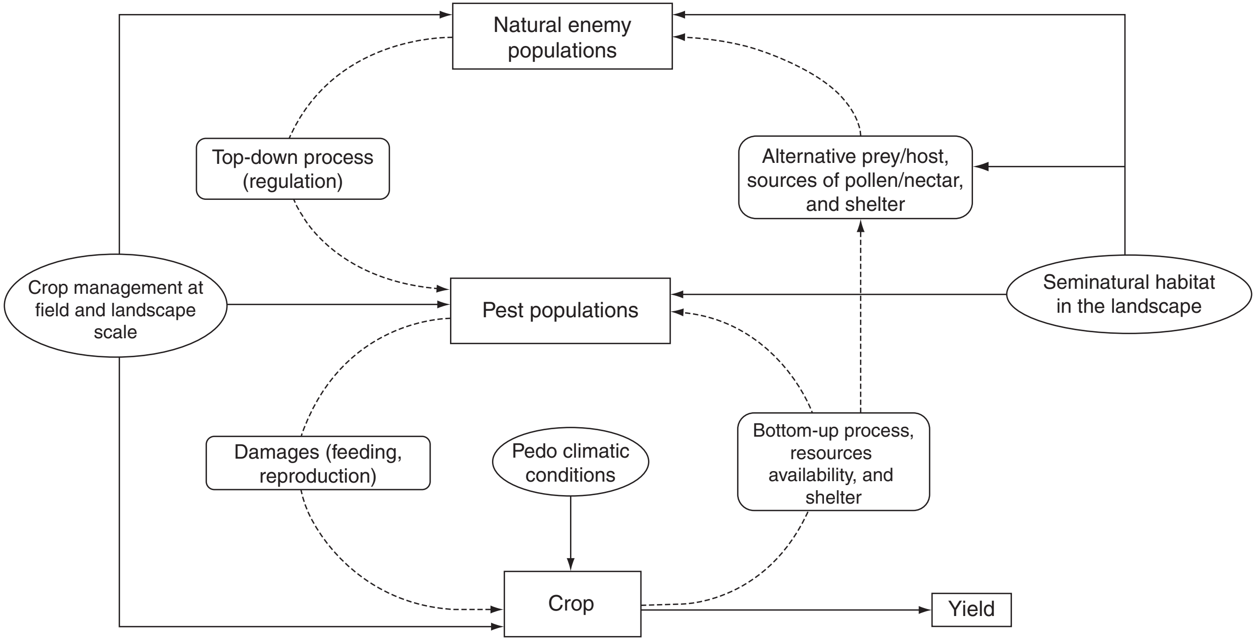

Figure 1 The potential effects of crop management and seminatural habitats on each level of a tritrophic chain (solid lines). Dotted lines represent the trophic interactions between each element of the tritrophic chain. Adapted from Gurr *et al.* (2003).

3.1. Alternative hosts and prey

Noncrop habitats maintain populations of alternative hosts and prey for the parasitoids and predators of crop pests (Denys and Tscharntke, 2002; Kozar *et al.*, 1994; Pickett *et al.*, 2000; Sotherton, 1984; Wyss, 1996). This enhances natural pest control by providing the natural enemies of pests with alternative hosts and prey during periods in which host and prey density is low in fields, or by increasing the fitness of natural enemies. For example, Bianchi and van der Werf (2004) showed, by modeling, that if the infestation of wheat by pest aphids is delayed, populations of the generalist predator *Coccinella septempunctata* become increasingly dependent on aphid populations in noncrop habitats. Ladybeetle populations are more vulnerable to periods of food shortage when prey availability in noncrop habitats is low (Bianchi and van der Werf, 2004). However, natural enemy population may increase spectacularly following the infestation of crops with pests, leading to a spillover effect, with these insects moving to seminatural habitats, where they may decrease the prey populations of other nonpest species (Rand *et al.*, 2006), thereby potentially decreasing the size of populations of beneficial secondary zoophagous species. The dependence of natural enemy populations on alternative prey or hosts is greater for generalist predators that may feed upon a variety of prey species than for specialist predator species.

Many parasitoids and other natural enemies consume honeydew (Wäckers *et al.*, 2005). The presence of sap-feeding alternative prey in noncrop habitats may therefore enhance the control of crop pests. For example, Evans and England (1996) found that levels of alfalfa weevil parasitism (*Hypera postica*) by the ichneumonid wasp *Bathyplectes curculionis* were higher when pea aphids were present. Indeed, access to pea aphid honeydew appeared to increase both the fecundity and adult life span of the wasp significantly. Alternative prey may also enhance the biological control of pests because they decrease intraguild predation (i.e., predation among predators that shares the same prey species) (Dinter, 2002). Meyhofer and Hindayana (2000) also showed that, when provided with alternative prey, such as unparasitized aphids, parasitoid mortality due to consumption of mummified aphids by predators diminished.

However, habitats providing alternative hosts or prey may also accommodate pest species, thereby increasing pest populations. Indeed, Lavandero *et al.* (2006) demonstrated that floral resource subsidies may have various effects on phytophagous insects and their natural enemies. Some plant species increase the fitness of herbivores and parasitoids, whereas other species selectively enhance the fitness of parasitoid. Wyss (1996) reported similar effects on different insect pests, but Pfiffner and Wyss (2003) showed that sown wildflower strips increase the fitness of natural enemies of crop pests sufficiently to contain the increase in pest populations, which may also benefit from the wildflower strips.

3.2. Alternative sources of pollen and nectar

Seminatural habitats also act as sources of pollen and nectar, which are essential for many species (Pickett and Bugg, 1998; Wäckers *et al.*, 2005). Several studies have shown that more diverse vegetation, including flowering weeds, for example, results in a greater availability of pollen and nectar, leading to higher densities of carabid beetles (Lys *et al.*, 1994), syrphid flies (Hausammann, 1996; Sutherland *et al.*, 2001), and parasitoids (Patt *et al.*, 1997; Powell, 1986). It has also been shown that many hymenopteran parasitoid species feed on floral nectar (Jervis *et al.*, 1993; Wäckers, 2001) and that this may lead to higher rates of parasitism (Berndt *et al.*, 2006; Ellis and Farrell, 1995; Stephens *et al.*, 1998). For example, Winkler *et al.* (2006) reported that nectar feeding is of crucial importance for the survival and fecundity of *Diadegma semiclausum* in field conditions. They showed that parasitism rates were very low if female parasitoids were deprived of nectar, and much higher if females were supplied with sufficient food. Wäckers (2001) compared the patterns of sugar used by the parasitoid *Cotesia glomerata* and its phytophagous host, *Pieris brassicae*. He found that the parasitoid used more types of sugar than its host and that some sugars increased the life span of the parasitoid by a factor of 15, whereas host life span was increased by no more than a factor of three. He also found that some sugars were of nutritional benefit to the parasitoid but not to *P. brassicae*.

3.3. Shelter and overwintering areas

Woody habitats often provide a more moderate microclimate than the center of fields, protecting natural enemies against extreme temperature variations (Landis *et al.*, 2000; Rahim *et al.*, 1991). Various studies have explored the impact of the proximity of noncrop habitats and have shown that parasitism levels of insect pests are higher and close to the edges of fields bordering noncrop habitats than in the center of fields due to a moderate mild microclimate and nectar availability (Altieri and Schmidt, 1986; Landis and Haas, 1992; Thies and Tscharntke, 1999). Seminatural habitats also provide natural enemies and pests with good conditions for overwintering, determining their spatial distribution in the spring. For instance, they allow *Episyrphus balteatus*, a major aphid predator syrphid fly, to overwinter at different stages in various types of shelter. It overwinters as adult females along southern edges of fragmented forests and at final larval stage along northern ones where aphids developed in the fall, thus determining its spatial distribution in the spring (Sarthou *et al.*, 2005). According to Keller and Häni (2000), 9 in every 10 auxiliary species require a noncrop environment at one stage of their life cycle, whereas this is the case for only one in two pest species. Most auxiliary species are, therefore, heavily dependent on the resources provided by seminatural areas, requiring them to travel back and forth between uncultivated habitats and crops. However, even if noncrop habitats appear to be less important for insect pest species than for natural enemies, they may nonetheless have a major effect on pest population dynamics, particularly during the overwintering period. Indeed, several studies have reported the overwintering of pest species in uncultivated areas (Leather, 1993; Pywell *et al.*, 2005). Pywell *et al.* (2005) identified several oilseed rape pest species (*Phylotreta atra*, *P. undulate*, and *Meligethes aeneus*) in hedgerows and field margins, and showed that the abundance of these pests was greater in the hedgerow habitat than in field margins. Of the six major pests of oilseed rape crop (i.e., pollen beetle (*M. aeneus*), brassica pod midge (*Dasineura brassicae*), cabbage seed weevil (*Ceutorhynchus assimilis*), cabbage stem weevil (*Ceutorhynchus pallidactylus*), rape stem weevil (*Ceutorhynchus napi*), and cabbage stem flea beetle (*Psylliodes chrysocephala*)), only two species, the brassica pod midge and the rape stem weevil, are not dependent on seminatural habitats for overwintering or summer diapause. These two pests emerge from the previous year's oilseed rape fields, and the brassica pod midge may even emerge from fields on which oilseed rape has been grown in the last 4 years (Alford *et al.*, 2003). Leather (1993) also demonstrated that a major cereal pest, the aphid *Sitobion avenae*, overwinters on perennial grasses. However, Vialatte *et al.* (2007) showed that the populations of this species (on cereals and on field margins) remain genetically separated. This strongly suggests that fields are not colonized by *S. avenae* from the field margins, but by aphids coming from early sown wheat crop and crop volunteers.

3.4. Interface between crop and seminatural habitats

The agroecological functions of seminatural habitats described earlier have highlighted the complementary nature of crop and noncrop areas for pests and their natural enemies, and emphasized therefore the role of habitat edges. Rand *et al.* (2006) hypothesized that the resources present in one type of habitat may subsidize shared consumers such that they have a greater impact on resources in the second type of habitat. Seminatural habitats have been seen as important sources of natural enemies that spread into crop fields, potentially enhancing the biological control of pests if in close enough proximity to the field. The variety of resources available in seminatural habitats allows the development of beneficial arthropod populations, which then spill over into crop fields (Tscharntke *et al.*, 2007). Indeed, empirical and modeling studies have demonstrated that the quality and quantity of seminatural habitat patches adjacent to the crop may affect top-down control (Bianchi and Wackers, 2008; Olson and Wackers, 2007). However, Rand *et al.* (2006) demonstrated that spillover effects from agricultural to seminatural habitats may also occur, highlighting several mechanisms. There is evidence that the primary productivity of the habitat determines the direction of spillover effects. Areas of low productivity are strongly affected by spillover effects from more productive habitats. Indeed, highly productive systems, such as cultivated areas, support higher prey densities, resulting in larger natural enemy populations and higher rates of emigration to less productive habitats by passive diffusion. It has also been shown that the temporal dynamics of resources across the landscape, particularly between cultivated and seminatural habitats, greatly affects the size and direction of spillover effects. Indeed, resources in the agricultural landscape vary strongly over time, as cultivated habitats provide high-quality resources for only part of the year. The abrupt decline in habitat quality due to harvesting leads to the active emigration of predators from the cultivated areas toward more stable seminatural habitats. Rand *et al.* (2006) explained that spillover effects may also result from complementation between the resources in seminatural and cultivated areas. The access to resources in both types of habitat and the positive effects of this complementation on fecundity and longevity may account for the greater aggregation of predators and stronger top-down control near field edges.

3.5. Effect of landscape context on biological control

Published studies on insect pest dynamics have shown that herbivore and natural enemy populations often respond to a spatial scale encompassing the crop or seminatural habitat patch and various temporal scales. Seminatural habitats have been shown to be key elements for species development and survival. These habitats serve as the starting point for field colonization to various extents by many species that are beneficial, damaging, or neutral to crops (Dennis and Fry, 1992; Denys and Tscharntke, 2002; Marshall, 2004; Nentwig, 1988; Thomas *et al.*, 1992). The distance between fields and seminatural areas and their spatial organization are therefore important in determining insect population dynamics. Most of the studies have adopted a dichotomous approach, considering crop and noncrop habitats in their analyses of the influence of the landscape on pest and natural enemy populations. Bianchi *et al.* (2006), in a review, tested the hypothesis that biological control of herbivores is enhanced in complex landscapes with a high proportion of seminatural habitats. They analyzed 28 studies focusing on pest pressure and/or natural enemy populations as a function of landscape composition, for various crops. They found that pest pressure was lower in complex landscapes, in 45% of the 10 studies they reviewed. They also found that natural enemy activity was enhanced by complex landscapes in 74% of the studies reviewed (24 publications). In 21% of the studies reviewed, no effect of landscape composition was reported, whereas in 5%, natural enemy activity was lower in complex than in simple landscapes. Thus, although most of the studies showed higher natural enemy activity, only 45% of them showed this to have reduced pest pressure in more complex landscapes. This indicates that there is considerable variability in the responses of organisms to landscape structure, with landscape complexity having no clear effect on pest suppression. Ever since this review was conducted, various studies have explored the impact of landscape diversity on natural enemy and pest populations, confirming these general conclusions. All six studies focusing on the impact of landscape diversity on natural enemies (parasitoids, beetles, and spiders) found that landscape complexity significantly increases natural enemy richness or abundance (Bianchi and Wäckers, 2008; Drapela *et al.*, 2008; Gardiner *et al.*, 2009; Marino *et al.*, 2006; Oberg *et al.*, 2008; Perović *et al.*, 2010). Five studies published since 2006 dealing with the effect of landscape context on insect pest abundance or damage reported various responses to landscape organization (Grilli and Bruno, 2007; Perović *et al.*, 2010; Ricci *et al.*, 2009; Valantin-Morison *et al.*, 2007; Zaller *et al.*, 2008b). These studies focused on pest of various crops, including oilseed rape, corn, or orchards. Landscape complexity was not assessed directly, but pest abundance or damage was found to be related to landscape variables that could be interpreted in terms of landscape complexity. For example, Grilli and Bruno (2006) found that the abundance of the corn planthopper (*Delphacodes kuscheli*) increased with the abundance and connectivity of its host patches. Thus, a simple landscape with a high proportion of the area under corn tends to support higher pest pressures than a more complex landscape. Conversely, in their study of oilseed rape pests, Zaller *et al.* (2008b) demonstrated that pollen beetle and brassica pod midge pressures decreased with increasing host patch abundance and increased with increasing abundance of noncultivated areas. In this case, more complex landscapes seem to enhance pest pressure. Moreover, conflicting results concerning landscape effects on pest populations have been published. For example, three studies have reported three different effects of landscape context on pollen beetle dynamics (Thies *et al.*, 2003, Valantin-Morison *et al.*, 2007, Zaller *et al.*, 2008b). Thies *et al.* (2003) found that pollen beetle was not affected by oilseed rape abundance in the landscape, whereas Valantin-Morison *et al.* (2007) demonstrated a positive effect of host areas and Zaller *et al.* (2008b) reported a negative effect. Moreover, Thies *et al.* (2003) found a negative correlation between landscape complexity and pest damage, whereas Zaller *et al.* (2008b) found a positive relationship between pest abundance and landscape complexity. Thus, the variability of responses of insect pests to landscape complexity reported in the previous studies appears to be multifactorial and not completely understood, implying further studies on pest populations to understand general patterns. Indeed, it depends on biological characteristics of pest species when different pests are involved, methodological differences between studies, geographic position of the studied areas, the way in which the landscape is described (e.g., grain of resolution), and the effect of farming practices dispatched within the landscape. Another complex effect that can be observed in conservation biological control studies is that potential pest species may benefit from conditions at the local or landscape scale that also favor natural enemies (Lavandero *et al.*, 2006; Perović *et al.*, 2010).

In landscape-scale studies, the relationships between arthropod populations and seminatural habitats within the landscape have generally been explored through a landscape composition approach (i.e., in terms of proportions of each type of land uses). However, such approaches do not take into account the spatial arrangement of land uses (i.e., the functional connectivity) and their specific effects on populations (e.g., the effects of the landscape matrix on dispersal activity). We found one study that investigated the effects of spatial arrangement on biological control, using a cost–distance approach in which land-use types can be assigned different costs to represent the degree of favorability for a given species (Perović *et al.*, 2010). In this study, the authors found various responses to functional connectivity in the landscape depending on the species considered. However, they concluded that the spatial arrangement of noncrop areas has a stronger effect than does noncrop proportions alone on natural enemy abundance with large dispersal abilities. According to the authors, the cost–distance approach makes it possible to identify both suitable habitats in the landscape and the spatial configuration of these habitats, to enhance colonization by natural enemy populations. Therefore, assessing functional connectivity of the landscape and its influence on biological control interactions appears to be an interesting approach for habitat manipulation and pest management strategies.

4. NATURAL ENEMY BIODIVERSITY AND INSECT PEST SUPPRESSION

Exploration of the relationships between natural enemy biodiversity and the suppression of arthropod herbivores is of crucial importance in our comprehension of the value of biodiversity and its impact on ecosystem services. Duelli and Obrist (2003) reported that for short-term pest control considerations, the abundance of beneficial organisms may appear more important than species richness, because prey and hosts are reduced by the number of antagonistic individuals rather than by species number. However, with a longer-term perspective, maintenance of a high diversity of natural enemy species is certainly more important than abundance, as a high functional diversity increases the stability of ecological functions and insures resilience (i.e., the capacity of the system to withstand disturbances and reorganize itself after perturbations) (Bengtsson *et al.*, 2003; Tilman, 1996). The regulation of insect pest populations in agricultural landscape may, therefore, result in trade-offs between natural enemy abundance and richness. Various effects of natural enemy diversity on herbivores suppression have been proposed in the literature. Recently, Letourneau *et al.* (2009) have summarized the main possible emergent effects of higher natural enemy biodiversity on pest suppression which can be positive, negative, or neutral:

- Herbivore mortality resulting from different natural enemy species can be equal (additive) or greater (synergetic) than the summed mortality caused by each species. This outcome is based on the species complementary model which includes resource-use differentiation such as predation at different life stages, at different periods in the season, or at different spatial positions, or foraging in ways that facilitate predation by other species.
- As it has often been observed that one natural enemy species can cause most of the mortality of a given herbivore, then the sampling effect model suggests that if the natural enemy diversity increases, the probability that this superior species will be present, increases too. However, negative sampling effect may also occur, because the probability of including a strongly disruptive natural enemy may increase as species richness increase (Loreau and Hector, 2001; Straub *et al.*, 2008).
- The insurance model suggests that the more natural enemy species are present, the greater are the chances to establish and maintain positive interactions among natural enemy species, cover heterogeneous conditions, and overcome potential negative interactions (Yachi and Loreau, 1999).
- Negative interactions among natural enemy species, such as intraguild predation (i.e., predation among predators that share the same prey species), hyperparasitism (i.e., the development of a secondary parasitoid at the expense of a primary parasitoid which already parasitized a host insect), or behavioral interference, may have subtractive effects on herbivore mortality.
- Neutral effects of increasing natural enemy diversity on pest suppression can be observed due to minimal interactions among natural enemy species or by canceling the effects of positive and negative interactions. Such effects are expected to occur when natural enemy species are functionally redundant (Straub *et al.*, 2008).

In the literature, a large number of studies have reported evidences for each of these possible effects (Finke and Denno, 2005; Rosenheim, 2007; Schmitz, 2009; Snyder *et al.*, 2006; Straub and Snyder, 2006; Wilby *et al.*, 2005). In order to synthesize the state of the art on the relationships between natural enemy biodiversity and herbivore mortality in different ecosystems, Letourneau *et al.* (2009) performed a meta-analysis on this topic. Their results highlight the importance to take natural enemy biodiversity into account in agricultural systems when interested in insect pest control.

Moreover, they clarify the general pattern of response of herbivores to higher natural enemy biodiversity in agricultural areas. The authors found that almost 70% of the studies reviewed (a total of 266 studies) reported more effective control for higher levels of natural enemy richness, suggesting that positive, complementary interactions between natural enemy species predominate over negative, antagonistic interactions. Negative interactions, such as intraguild predation, can be reduced in complex-structured vegetation and complex food webs, respectively, through avoidance between natural enemies and higher prey and host availability (Finke and Denno, 2002; Meyhöfer and Hindayana, 2000). Therefore, these important results suggest that conservation of natural enemy biodiversity and pest control are compatible with each other and, in many cases, complementary goals (Straub *et al.*, 2008). However, the potential negative effects that may occur in some cases imply to always consider pest populations and effective biological control to examine effects of natural enemy diversity in conservation biological control studies. Letourneau *et al.* (2009) reviewed studies carried out in different ecosystems ranging from natural to agricultural systems, and were therefore able to compare the strength of the relationship between natural enemy diversity and herbivore suppression in each type of system. They found that there was no statistical significant relationship between higher natural enemy diversity and herbivore suppression in natural systems, but that this relationship was very strong in agricultural systems, suggesting an important potential biological control in these systems. These results are consistent with the conclusions of Halaj and Wise (2001) who found that removing predators of herbivores led to higher plant damage in agricultural systems than in natural systems.

5. Effects of Crop Management on Pests and their Natural Enemies

Unlike seminatural habitats, arable fields are generally thought to be subject to major disruption due to agricultural practices. Pest and natural enemy populations may depend on arable fields as a source of potential hosts or prey, pollen and nectar resources, and diapause or overwintering areas. This dependence is particularly strong when the proportion of seminatural habitats in the landscape is low. In this case, natural enemies are highly susceptible to the effects of crop management at the field scale. We provide here a concise overview of the main crop management effects on each element of a trophic chain with three levels: the plant, the phytophagous pest, and its natural enemy (Fig. 1). Each trophic level is represented here at the population or community level.

5.1. Within-field diversity

Within-field diversity is known to have a major impact on trophic interactions and biological control (Andow, 1991). In a review, Andow (1991) identified 209 published studies dealing with the relationships between vegetation diversity and phytophagous arthropod species. Of the 287 phytophagous species identified in these studies, 52% appeared to be less abundant in diversified agroecosystems than in monocultures, whereas 15% were found at higher densities in diversified systems. Indeed, crop monocultures are environments in which it is difficult to establish efficient biological pest control, because the resources they provide are insufficient to ensure that natural enemy populations perform well. Thus, increasing diversity in the field by intercropping, cover cropping, or even tolerating weeds may enhance biological control and reduce the damage resulting from insect pest attacks. Many studies have tested this hypothesis and shown that higher crop diversity significantly reduces pest damage (Nickel, 1973; Norris and Kogan, 2005; Perrin, 1977; Risch, 1983; Vandermeer, 1989). Various hypotheses have been put forward to explain the potential mechanisms involved in interactions between within-field diversity and pest damage. Pimentel (1961), and then Root (1973), developed the "Enemy Hypothesis", according to which, the observed decrease in the number of herbivores in intercropped results partly from the attractiveness of the intercrop for more abundant and/or efficient predators and parasitoids, presumably because more resources and habitats are available than in monocultures. Tahvanainen and Root (1972), and then Root (1973) also developed an alternative "Resource Concentration Hypothesis," according to which, the probability of herbivores finding their host plant, remaining on that plant, and reproducing on it is higher in monocultures than in mixtures of several species in which the resource is diluted among other resources. This hypothesis is based on chemical and/or physical confusion of the pest due to mixed cues (the Disruptive Crop Hypothesis, Vandermeer, 1989). Finally, the presence of a second crop within or close to the principal crop may also lead to high herbivores densities on the second crop, thereby lowering the incidence of herbivores on the main crop (the Trap Crop Hypothesis, Vandermeer, 1989). However, higher within-field diversity does not always result in better pest control. Increasing diversity may also aggravate pest problems (Andow, 1991) or hinder beneficial insect activity (Andow and Risch, 1985), as it may enhance interspecific competition or intraguild predation (Broatch *et al.*, 2010).

5.2. Host plant resistances

Host plant resistance has been shown to decrease herbivore population development and/or the damage caused by pests significantly (Francis *et al.*, 2001; Sharma and Ortiz, 2002; Van Emden, 1991). There are two major types of resistance: induced resistance (triggered by extrinsic biotic or abiotic factors) and constitutive resistance (always expressed) (Kogan, 1994). Both types of resistance directly affect herbivore populations through antixenosis, antibiosis, or tolerance. The effects of host plant resistance on entomophagous insects are well documented for interactions in a three-level trophic system, and several mechanisms have been highlighted. For example, Brewer *et al.* (1998) reported that parasitoid populations were larger on susceptible barley cultivars than on cultivars resistant to aphids, due to the larger aphid populations on susceptible cultivars. However, parasitism rates were similar for the two cultivars. This density-dependent effect is not the only mechanism, and plant resistance often affects herbivorous species development, fecundity, and population growth. Since natural enemies, particularly parasitoids, select their host depending on weight, size, or growth stage, plant resistance may indirectly affect the biological control of pests. Regarding predation, different aphid host plants can directly affect predator development by supplying preys with different nutritional values. Similarly, different crop habitats may affect the biological traits of predators at the individual or community level, by modifying the abundance of prey available (Bommarco, 1999). Kogan (1994) reviewed the benefits and pitfalls of using host plant resistance as a single pest management factor. Specificity, cumulative efficacy, potential compatibility with other tactics, and persistence were among the advantages of plant resistance identified. However, this approach was also found to be subject to a number of drawbacks, including the time required to develop resistant varieties, genetic limitations, and conflicting resistance traits.

5.3. Nitrogen fertilization

Several studies have shown that herbivorous insects usually select their host plants on the basis of potential quality as a host and as a source of food (Dosdall *et al.*, 1996; Finch and Collier, 2003; Hopkins and Ekbom, 1996; Moon and Stiling, 2000). Moreover, plant resistance to insect pests varies considerably with age, growth stage, and physiology of the plant (Altieri and Nicholls, 2003). Nitrogen fertilization may, therefore, play an important role in population dynamics and performances of herbivores by affecting plant resistance, host selection mechanisms, or the ability of plants to recover from the damage inflicted by herbivores. Two hypotheses have been initially developed to account for the interactions between host plant quality and pest populations: the Plant Stress Hypothesis and the Plant Vigor Hypothesis. According to the Plant Stress Hypothesis, physiologically stressed plants are more susceptible to pest attacks due to (i) direct effects, such as improvements in the nutritional quality of the plant (e.g., increase in amino-acid content) or a decrease in its resistance mechanisms, or (ii) indirect effects, such as reduced efficiency of natural enemies (White, 1984). According to the Plant Vigor Hypothesis, many herbivores preferentially feed on vigorous plants, because they provide a better source of food (Price, 1991). Several studies have provided evidence supporting these two hypotheses, for a wide range of herbivores (Bruyn *et al.*, 2002; Craig and Ohgushi, 2002; Dosdall *et al.*, 2004; Jones and Coleman, 1988; Mattson and Haack, 1987). Although these two approaches are competing paradigms and that no general pattern is emerging from the literature, both argue that plant physiological status and plant growth are important determinants of the damage inflicted by insect pests, highlighting the major role of plant nitrogen content. According to Pimentel and Warneke (1989), variations in the responses of pest populations to nitrogen fertilization may be explained by differences in the feeding behavior of herbivores.

Scriber (1984), in a review of 50 years of research on crop nutrition and insect attack, identified 135 studies reporting higher levels of damage and/or growth for leaf-chewing insects or mites in high nitrogen-fertilized crops, versus fewer than 50 studies in which herbivore damage was reduced by normal nitrogen fertilization. Waring and Cobb (1992), in a review of 186 studies investigating insect and mite responses to soil or host plant nutrient levels, reported a similar pattern, with a predominance of positive responses to nitrogen fertilization among herbivores (60% of the studies).

Recent studies have focused on the effect of plant fertilization and quality on the third trophic level (i.e., the natural enemies). Sarfraz *et al.* (2009) studied the effect of fertilization on the oilseed rape pest *Plutella xylostella* and its parasitoid *Diadegma insulare*. They demonstrated that *D. insulare* performed better on plants grown with high levels of fertilizer and that the proportion of *P. xylostella* escaping control by *D. insulare* was higher on plants with low levels of fertilizer. In this study, the quality of the plants on which *P. xylostella* hosts were reared significantly affected developmental times of both female and male *D. insulare*. Investigations of the effect of nitrogen fertilization on the different trophic levels and on tritrophic interactions are therefore important, as they highlight the complex bottom-up effects to be taken into account in integrated pest management approaches.

5.4. Tillage

Soil tillage is known to have major effects on the local habitat, soil-inhabiting organisms, and relationships between organisms (El Titi, 2003; Kladivko, 2001; Stinner and House, 1990). In particular, the intensity of soil tillage, the method used, the number of operations, the frequency, and the period of soil cultivation seem to have an impact on predatory arthropods. Reduced tillage systems create a more stable environment, encouraging the development of more diverse species (including decomposer communities) and slower nutrient turnover (Altieri, 1999). The general pattern is that both the abundance and diversity of the soil fauna tend to increase with decreasing tillage intensity (Cárcamo, 1995; Holland, 2004; Kendall, 2003). However, species differ in their response to soil tillage and local habitat disturbance sometimes in opposite ways. Indeed, the response observed is highly dependent on the ecological characteristic of the species concerned, such as body size, life cycle, diet, dispersal abilities, and population size (Baguette and Hance, 1997). Many of the species inhabiting fields may be able to withstand some degree of soil disturbance, but certain life cycle stages, such as pupae, less mobile larvae, and estivating or hibernating adults, are particularly vulnerable (Kendall, 2003). Different patterns of response to soil tillage have been reported: direct effects on natural enemies, especially parasitoids, due to mechanical damage, greater exposure to predation, or the immediate emigration of arthropods to adjacent habitats. Soil cultivation may also have indirect effects on arthropod predators by modifying habitat quality, removing microhabitats for reproduction, or decreasing prey densities. The crop residues left on the soil in reduced tillage systems may indirectly impact herbivore and predator populations, respectively, through physical barrier effects altering host location and increases in organic matter availability which enhances size, diversity, and activity of predators (Kladivko, 2001). Soil tillage has been shown to reduce significantly the abundance of various invertebrates, such as epigeic earthworms (Chan, 2001) and springtails (Petersen, 2002), which may serve as an alternative prey for many polyphagous predators. Reductions in such populations due to intensive tillage may therefore have an indirect effect on predator populations. Thorbek and Bilde (2004) studied the effects of different mechanical crop treatments on generalist predator arthropods and have found that these indirect effects (i.e., habitat deterioration) of soil cultivation may have a stronger overall impact on arthropod dynamics than direct mortality. They also demonstrated that soil cultivation and grass cutting cause the direct and indirect mortality and emigration of generalist predator arthropods, including spiders, in particular. The effects of postharvest soil tillage on parasitoid populations have been studied principally in the case of oilseed rape crop. Nilsson (1985) showed that inversion tillage strongly affects the survival and emergence rates of parasitoids overwintering in the soil. Soil tillage may therefore have an indirect effect on the rates of parasitism of oilseed rape pests in the following year. For example, Ferguson *et al.* (2003) found that although 24% of the *M. aeneus* pest population was parasitized, fewer than 2% of the parasitoids survived over winter to emerge as adults in the following spring, indicating a strong impact of soil cultivation on natural enemy populations.

5.5. Sowing date, plant density, and harvesting date

Sowing date is known to affect the level of damage resulting from insect pest attacks and the ability of plants to compensate for this damage. Dosdall and Stevenson (2005) demonstrated a strong effect of oilseed rape sowing date on flea beetle (*Phyllotreta cruciferae*) damage. Indeed, greater damage was observed on spring-sown oilseed rape than on fall-sown oilseed rape. The damage to oilseed rape apical meristems inflicted by flea beetles may prevent a compensatory response, but by the time of greatest injury, crops have enlarged apical meristems, making them less susceptible to damage. Oilseed rape sown in the fall is able to progress beyond the vulnerable cotyledon stage by the time that flea beetles inflict the most damage, resulting in less crop damage. A similar effect has been reported for corn. Early-sown corn is less susceptible to corn earworm and stem borer, *Diatrae grandiosella* (Bajwa and Kogan, 2004). This lower susceptibility results from the tendency of *D. grandiosella* to lay fewer eggs on more mature plants, which have already passed their critical growth stage before most of the larvae begin to feed (Herzog and Funderburk, 1985). However, studies of insect pest community may reveal antagonist effects of sowing date. For example, Valantin-Morison *et al.* (2007) have shown that the early sowing of winter oilseed rape tends to increase cabbage root fly (*Delia brassicae*) damage, but is associated with a lower level of attack by cabbage stem flea beetle (*P. chrysocephala*). Differences in the functional composition of invertebrate assemblages between sowing seasons have been reported in arable systems, consistent with a direct effect of sowing date on predator communities (Douglas *et al.*, 2010; Hawes *et al.*, 2009). However, the impact of sowing date on top-down control has yet to be evaluated.

The original Resource Concentration Hypothesis (Root, 1973; Tahvanainen and Root, 1972) predicted an increase in herbivore density per host plant with increasing plant density. However, despite the confirmation of this hypothesis in many cases (Andow, 1991), several recent studies have invalidated this prediction (see Yamamura, 1999, for a review), providing support for a Resource Dilution Hypothesis (Otway *et al.*, 2005; Rhainds and English-Loeb, 2003) associated with different patterns of responses. For example, Valantin-Morison *et al.* (2007) found a negative correlation between plant density and oilseed rape damage due to root maggot, cabbage stem flea beetle, and pollen beetle.

Harvesting produces a brutal perturbation of the agroecosystem involving microclimate changes that affect natural enemy populations. According to Riechert and Lockley (1984), harvesting has a greater effect on spider communities than the use of pesticides. The effects of harvesting depend on its timing. For spring crops (such as corn), harvesting occurs sufficiently late for most of the predatory species to be at the end of their period of activity and to have reached their overwintering sites. For winter crops (such as winter oilseed rape and most cereals), harvesting dates generally coincide with the period during which the abundance and activity of some predators are maximal (Büchs, 2003).

5.6. Crop rotation

Rotation of annual crops has been empirically developed by farmers to reduce and control soil-borne pests and disease proliferation. By the mid-twentieth century, a well-developed rotation consisted of six to eight different crops in sequence (Häni *et al.*, 1998). An increase in economic pressure and food demand led farmers to make greater use of pesticides and to maximise land use. The rotation was reduced to a few species, leading to an increase in pest proliferation and a decrease in biodiversity of beneficial species. Büchs *et al.* (1997) studied the effects of different crop rotation intensities on the arthropod community in a sugar beet rotation and an oilseed rape rotation. They showed that certain pest species were favored by an increase in the intensity of crop rotation, whereas some beneficial insects were unable to establish stable populations in arable crops with intensive rotations. The authors found that the number of individuals, species richness, body length, and reproductive rates of beneficial insects increased with the progressive extensification of crop sequences, particularly in set-aside areas subjected to natural succession. O'Rourke *et al.* (2008) studied the effects of rotations on ground beetle populations, by comparing assemblages between a system involving conventional chemical and a 2-year rotation system, and a system with low-input levels and a 4-year rotation. They reported the same response pattern as Büchs *et al.* (1997): carabid beetle activity density and species richness were higher in the low-input, 4-year rotation than in the conventionally managed, 2-year rotation.

5.7. Pesticide use

Pesticides have been widely studied and have been shown to have a negative effect on natural enemy populations in many different studies (Chabert and Gandrey, 2005; Koss *et al.*, 2005; Langhof *et al.*, 2003; Tietjen and Cady, 2007). Both direct and indirect effects on the third trophic level have been highlighted. For example, Ulber *et al.*, (2010) have demonstrated that many parasitoid species of oilseed rape pests are directly affected by the late spraying of insecticides, at around the time of flowering and by aphid insecticide on wheat. Indeed, parasitoid populations emerge from previous year oilseed rape field (generally, wheat fields) 1–2 weeks before rapeseed flowering and are particularly active in the crop during flowering, searching for suitable hosts. Different studies have also proved an important detrimental effect of insecticide on the auxiliary fauna (such as spiders, carabids, staphylinids, syrphids, or parasitoids) (Dennis *et al.*, 1993; Gonzalez-Zamora *et al.*, 2004; Langhof *et al.*, 2003;Wang *et al.*, 1993). Walker *et al.* (2007) have provided evidence of indirect nontarget effects of the insecticides used to control the lettuce aphid, *Nasonovia ribisnigri*, on one of its predators, *Micromus tasmaniae*. Other studies have considered the impact of pesticide treatments on behavioral components and the recolonization abilities of beneficial arthropods (Desneux *et al.*, 2006; Salerno *et al.*, 2002). For example, Salerno *et al.* (2002) demonstrated changes in the behavior of insecticide-treated parasitoids that might influence their foraging ability and parasitism rates, due to changes in their response to host cues. Desneux *et al.*

(2006) reported reductions in the recolonization abilities of adult parasitoids from treated crops. Various studies have also demonstrated an indirect negative effect of herbicide applications on invertebrate populations through the reduction of weeds and the resources they provide (Brooks *et al.*, 2003; Heard *et al.*, 2006). Finally, it has been demonstrated at a very large scale that pesticide use reduces the opportunities for biological pest control in agroecosystems throughout Europe, where agricultural intensification has been promoted for several decades (Geiger *et al.*, in press).

6. GENERAL EFFECTS OF FARMING SYSTEMS ON NATURAL ENEMY BIODIVERSITY, PESTS, AND SUBSEQUENT BIOLOGICAL CONTROL

In the light of the previous results, the relationships among farming systems, natural enemy diversity, and insect pest suppression appear to be a key element in our understanding of natural pest control mechanisms. In the last decade, an increasing number of studies have dealt with the impact of farming systems on the diversity and abundance of fauna, particularly as concerns species involved in natural pest control. Most of these studies have compared organic and conventional farming systems (sometimes, integrated farming systems), with the aim of evaluating the impact of organic farming on the diversity of different biological groups (Booij and Noorlander, 1992; O'Sullivan and Gormally, 2002). Hole *et al.* (2005), in a review of 76 studies, clearly demonstrated that the species abundance and/or richness of several taxa, ranging from plants to mammals and birds, tended to be higher on organic than on conventional farms. Bengtsson *et al.* (2005) analyzed the effects of organic farming in a meta-analysis of 66 publications comparing organic and conventional systems. They found that species richness was generally about 30% higher, on average, in an organic farm. Analysis of the effects of farming systems on different biological groups, such as birds, arthropods, soil organisms, and plants, revealed a heterogeneous response of species richness to farming systems. The species richness of predatory arthropods appeared to be increased by organic farming, whereas this was not the case for nonpredatory arthropods. Bengtsson *et al.* (2005) also reported a 50% increase in the species abundance of all organisms in organic farming systems, but with strong variations between groups: predatory insects, soil organisms, and plants responded positively to organic farming, whereas nonpredatory insects and pests did not.

However, even if organic farming systems tend to support higher levels of biodiversity (Bengtsson *et al.*, 2005; Hole *et al.*, 2005), this does not necessary imply that such systems provide more effective biological control of pests. A recent study (Macfadyen *et al.*, 2009a) analyzed the differences in natural pest control between organic and conventional systems, using a food web approach on a three-level food chain (plant, herbivore, and parasitoid) at the whole-farm scale. The authors showed that biodiversity for all three trophic levels was significantly higher on organic farms and confirmed the results of Bengtsson *et al.* (2005). They also highlighted significant structural differences in food webs between organic and conventional farms, with herbivores in organic farming systems being attacked by a larger number of parasitoid species than those on conventional farms. However, differences in biodiversity and food web structure between farming systems did not result in a better natural pest control on organic farms, because no difference in parasitism rates was found.

The response to farming systems is highly variable and depends on the life-history traits of the species concerned. Some of the elements influencing the abundance and diversity of biological groups are not particularly related to the type of farming system. It is therefore important to consider crop management and farming system features when trying to understand the interactions between natural enemy and herbivore populations. For example, the type of soil tillage is an important element determining the survival of natural enemies that is independent of the farming system. Moreover, several studies have demonstrated that organic farms tend to be located in more heterogeneous landscapes with higher proportions of seminatural habitats, smaller field sizes, and higher and wider less intensively managed hedgerows (Langer, 2001; Norton *et al.*, 2009). It is therefore also important to take into account the landscape context when considering the effects of cropping systems, so that the relative importance of these two aspects can be determined and confounding effects avoided. Indeed, Macfadyen *et al.* (2009b) found no significant difference in aphid parasitism rates between organic and conventional farming systems, probably because landscape context affected the results and was not taken into account in their study. They concluded that differences between systems may be more obvious in a more homogeneous landscape that brings out cropping system effects. Hole *et al.* (2005) highlighted several inconsistencies between studies, almost certainly due to the complexity of the interactions between environmental variables and between taxonomic groups. Indeed, other factors, such as location, climate, crop type, and species, are important elements affecting the relationship between farming systems and biological control.

7. INTEGRATING FARMING SYSTEMS, CROP MANAGEMENT AND LANDSCAPE CONTEXT TO UNDERSTAND BIOLOGICAL CONTROL MECHANISMS

7.1. Integrating farming system

As pointed out earlier, several studies have reported that organic systems tend to support higher biodiversity levels. Indeed, synthetic chemical insecticides have a major impact on natural enemies, pests, and general biodiversity

(Duffield, 1991; Koss *et al*., 2005). Several recent studies have thus integrated different types of farming systems (generally, organic vs. conventional) into landscape studies, to determine whether the landscape structure or the farming system is more relevant when investigating biological control interactions.

We therefore collected articles evaluating the impacts of both farming and landscape features on the activity of natural enemy populations. All these studies broke farming systems down into two main types: organic and conventional systems. Generally, pairs of organic and conventional fields embedded within the same landscape were selected to separate the effects of landscape and farming system. Landscapes were mostly described in terms of the percentage of noncrop elements in the landscape or the Shannon habitat diversity index. Different indices were used to quantify natural enemy populations in these studies: species richness, activity-density, parasitism rates, or natural enemy conditions. If different results were reported in a given study, due to an effect of the year or site, for example, we added a coefficient corresponding to the proportion of observations contributing significantly to the related effect (positive, negative, or neutral effect).

Few studies have reported both landscape and farming system effects on natural enemy populations and their potential for biological control. We identified nine studies (Clough *et al*., 2005, 2007; Eilers and Klein, 2009; Östman *et al*., 2001a,b; Purtauf *et al*., 2005; Roschewitz *et al*., 2005b; Schmidt *et al*., 2005; Weibull *et al*., 2003) on natural enemies of insect pests that considered these two factors simultaneously, but only three of them evaluated effective biological control (i.e., have also considered pest populations in the same study). Most of the studies dealt with natural enemies found in cereal fields and involved different types of organisms such as spiders, carabid beetles, staphylinids, and parasitoids. The effect of landscape was generally clear: more complex landscapes with high proportions of seminatural habitats promoted natural enemy populations in 83.3% of cases, and had no significant effects in 16.7% of the studies. The impact of the farming system was more heterogeneous. Indeed, in 50% of cases, the farming system had no particular effect on species richness or in activity density of the natural enemies. In 38.8% of studies, organic systems were found to have a positive effect on the species richness, activity density, or conditions of natural enemies. Negative effects of organic farming on natural enemy populations were also reported in 11.1% of the cases. Landscape context had a stronger effect than the farming system in 50% of cases. Only one study (11.1% of cases) (Clough *et al*., 2007) found that landscape context had no effect on natural enemies (Staphylinids). Both landscape composition and farming systems were found to have major effects on natural enemy richness, conditions, or activity density in 38.8% of studies.

Thus, these studies bring out variable results about natural enemies' response to farming systems and subsequent pest control. The effect of the surrounding landscape on natural enemies seems to be greater than that of the farming system. Bengtsson *et al.* (2005) reported a similar pattern in a study of biodiversity and abundance in organic agriculture. Farming systems only partly accounted for the variation in species richness, activity density, conditions, or parasitism rates, whereas landscape context effects predominated in the studies reviewed. Thus, these studies revealed that populations may be influenced by farming systems on a small scale and that differences between farming systems may result from behavioral responses and individual decisions (Bengtsson *et al.*, 2005), whereas landscape features provide information about population dynamics tightly linked to species biology and life cycle. Tscharntke *et al.* (2005), based on the results of Roschewitz *et al.* (2005a), explained that the influence of farming systems on species richness is more important in simple landscapes than in complex landscapes. According to the authors, the negative impact of conventional systems on species richness is only observed in simple landscape where colonization from the surrounding landscape is limited and therefore very much affected by local farming systems. Therefore, in those landscapes, improvement of the local systems may enhance general biodiversity and biological regulation of insect pest and may counterbalance the negative effects of intensive monoculture landscapes.

The classic opposition of different farming systems (organic vs. conventional) may be useful for deciphering general patterns, but it is probably not the most relevant approach for studying the impact of specific farming practices on particular pests and their natural enemies. Indeed, organic and conventional systems comprise a range of very different practices that may have different effects on population dynamics, as outlined earlier. The practices encompassed by organic and conventional farming systems may be sometimes very similar, at least in terms of their impact on biodiversity and trophic interactions. Many of the factors other than farming system that can influence abundance and diversity of natural enemies at the whole-farm scale may be under the control of farmers (e.g., hedgerow management) and are not always included in the analysis. Norton *et al.* (2009) showed that organic farms tended to be located in more heterogeneous landscapes with higher proportions of seminatural habitats and had smaller field sizes. The design of the study is therefore of crucial importance to prevent confounding effects when comparing farming systems at the landscape scale. Great care must be taken when selecting fields under different farming systems for studies about trophic interactions. Thus, we advocate, in studies about links between biodiversity and farming systems in general, and investigating trophic relations and biological control in particular, a clear description of cropping systems and an explicit consideration of seminatural habitats (quantitatively and qualitatively).

All the studies reviewed here considered the farming systems of the fields selected in the center of each landscape. However, it is probably very important to take into account farming systems within the surrounding landscape. Most studies of landscape context have not explicitly taken into account the other farming systems within the landscape. However, we found one study (Rundlöf *et al.*, 2008) in which the authors studied the effect, at both the local and landscape scales, of organic systems on butterfly species richness and abundance. They found that species richness and abundance were affected very differently on the two scales. Species richness and abundance were increased by organic farming at the local scale. However, the local species richness of both organic and conventional fields was positively influenced by the proportion of organic farming in the landscape. These authors also demonstrated that farming practices within fields had a stronger influence on butterfly abundance if the fields were surrounded by conventional rather than organic fields. Thus, in addition to taking into account seminatural habitats in the landscape and local farming systems, studies should also consider the spatial distribution of farming systems across the surrounding landscape, to determine the real effects of each explanatory variable and to prevent confounding effects.

7.2. Integrating crop management

As crop management greatly influences pests and their natural enemies at the local scale and that consideration of the farming system is not always the most relevant approach, several recent studies have focused on crop management variables and landscape configuration to understand insect pest or natural enemy dynamics. We identified seven studies focusing on the effects of crop management and landscape context on insect pests (Valantin-Morison *et al.*, 2007; Zaller *et al.*, 2008a,b) and on natural enemy populations (Drapela *et al.*, 2008; Elliott *et al.*, 1998; Prasifka *et al.*, 2004; Zaller *et al.*, 2009). In all these studies, landscape configuration always influenced pest (in terms of abundance or damage) or natural enemy populations (in terms of species richness, abundance, and activity density or parasitism rates). Various elements of crop management were investigated in these studies, depending on the characteristics of the species considered: sowing date, sowing density, pesticide use, crop height, crop coverage, within-field diversity, or soil quality. It is therefore difficult to determine the general impact of specific practices. However, the main contribution of this approach is that it makes it possible to quantify and, in some cases, to rank the impact of particular farming practices over landscape context effect. For example, Zaller *et al.* (2008b) found that the damage caused by pollen beetles and stem weevils was positively correlated with the soil quality of the field and with woody areas. Elliott *et al.* (1998) found that the abundance, species richness, and diversity of aphid predators increased with increasing within-field diversity, noncrop areas, and fragmentation in the landscape. They also demonstrated that landscape variables were included in regression models more frequently than within-field variables, and showed that they accounted for a greater percentage of variation in abundance of aphid predators. It is important to determine the relative impact of farming practices to ensure effective biological control within cropping systems, as these practices are more convertible elements than landscape elements. Moreover, such an approach made it possible to quantify the relative contributions of crop management, farming systems, and landscape variables at the different trophic levels. This ranking step appears to be an important stage, improving our understanding of natural pest control mechanisms and pest damage.

7.3. Interaction between farming practices and landscape context

The relative influence of the farming system and crop management on biological control is tightly linked to the spatial scale considered. Several authors studying the effects of landscape and farming systems on species richness and abundance reported interactions between landscape and local effects. They showed that organic or low-intensity farming systems have no or low effects on populations in complex landscapes, whereas they have a substantial influence in simple landscapes (Holzschuh *et al.*, 2007; Roschewitz *et al.*, 2005a; Rundlöf and Smith, 2006). This important interaction allows explaining why in 50% of the cases farming systems have no particular effects in our previous literature review about the effects of farming system and landscape context. This hypothesis has been originally formulated and confirmed in a study comparing farming systems on arable weed diversity in different landscape types (Roschewitz *et al.*, 2005a; Tscharntke *et al.*, 2005). As this interaction is increased by higher dispersal abilities of organisms, interactions between landscape context and particular crop management on natural enemy and biological control of insect pests may also occur. The important effect of the farming system or crop management in homogeneous landscapes is probably due to the local provision of resources, hosts, shelters, and more generally suitable conditions that enhance species richness and biological control. Local management effect may have lower effects in more complex landscapes, because the local species richness depends on the diversity of habitats and populations in the surrounding landscape (Tscharntke *et al.*, 2005). Thus, in homogeneous landscapes, local management, through adapted crop or field boundaries management, for example, may be an interesting way to enhance functional biodiversity and biological control.

8. CONCLUSIONS

Ecological studies provided a strong theoretical base of knowledge concerning the way in which species are likely to respond to landscape context and the establishment of population dynamics at the landscape scale.

However, such studies have generally not taken into account the diversity of cropping areas and their relative managements, assuming arable land to be homogenous. In our review of the effects of crop management on trophic interactions, we demonstrated that farming practices might play an important role in regulating natural enemy and pest populations at a local scale. A clear description of crop management in landscape studies therefore appears to be of crucial importance for identifying the key driver of biological control and ranking the effects of landscape, farming system, and farming practices. This is a fundamental step in the design and assessment of ecologically sound integrated pest management strategies for farmers. It is also important to evaluate the quality of seminatural areas in terms of agroecological functions for natural enemies and pests. Consideration of the habitat quality of crop and noncrop areas for pest and their natural enemies presents agronomists and ecologists with a real challenge in their attempts to design integrated pest management strategies for application at the landscape scale. Moreover, all the studies reviewed here focused on either crop management or the farming system at the local scale and did not consider farming practices over the entire landscape. However, the range of spatial and temporal scales experienced by pests and their natural enemies is likely to result in trophic interactions being influenced by farming practices in the surrounding landscape. If we are to understand how species react at the landscape scale, studies will need to take into account the detailed characteristics of seminatural habitats, local crop management effects, and landscape farming practices.

Integrated pest management paradigm holds that pests and their management exist at the crossroads of three major multidimensional fields of study: ecology, socio-economy, and agronomy, with ascending levels of complexity and expanding spatial scales (Kogan, 1998). Integrated pest management strategies may be seen as the complementation of different techniques to meet three main objectives: (i) a production purpose (crop performance and quality of products), (ii) socio-economic imperatives (farm organization, farm income), and (iii) environmental objectives (limitation of pesticide and nitrogen discharge into the environment, minimization of water, and energy use) (Kogan, 1998). The consideration of landscape features in biological control-based pest management strategies seems to be a relevant approach, although this assertion has not been clearly demonstrated, as studies on the effects of landscape and farming practices on natural pest control do not generally consider all the three objectives. Firstly, the enhancement of natural enemy populations does not necessarily imply effective pest control, and the relationships between crop and noncrop habitats are complex and may be antagonistic (e.g., Thies and Tscharntke, 1999; Valantin-Morison *et al.*, 2007; Zaller *et al.*, 2008a). Secondly, the effects of stronger biological control on productivity are unclear and the effects of landscape on pest populations and crop damage have rarely been documented (but see Östman *et al.*, 2003), even though they are much more relevant for crop production than any effect on natural enemies (Bianchi *et al.*, 2006).

The development of large-scale pest management strategies therefore requires a more holistic approach including the effects of both crop and landscape management. Such an approach would also fill in gaps in our knowledge about the ecology of insect pests (e.g., overwintering areas, pattern of migration) and quantify these effects in terms of environmental (e.g., energy use, pesticide use, and nitrogen discharge) and economic (e.g., crop damage, yield losses, and cost/benefit) consequences. The complementation of empirical studies and on-farm trials with modeling approaches is likely to prove an interesting strategy for improving integrated pest management and meeting this scientific challenge.

The service concept at the landscape-scale highlights the link between landscape patterns and human values (Termorshuizen and Opdam, 2009). It can be seen as a chain of knowledge connecting spatial structure, landscape functions, and human values. Studies about such services are therefore predisposed to integer socio-economic dimension and landscape actors or practitioners. However, whereas studies concerning the relationship between structure and functions are an established element of research, efforts need to be made to encourage the study of relationships between landscape function and human values (Termorshuizen and Opdam, 2009). Many studies at the landscape scale suffer from a lack of information about the real effects of crop management and higher levels of biodiversity on natural pest control and yields. Landscape-scale studies about biological control-based integrated pest management should therefore include and quantify the economic output of such strategies for farmers.

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