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Reprint of "Conservation biological control and enemy diversity on a landscape scale" [Biol. Control 43 (2007) 294–309] ☆

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Abstract

Conservation biological control in agroecosystems requires a landscape management perspective, because most arthropod species experience their habitat at spatial scales beyond the plot level, and there is spillover of natural enemies across the crop–noncrop interface. The species pool in the surrounding landscape and the distance of crop from natural habitat are important for the conservation of enemy diversity and, in particular, the conservation of poorly-dispersing and specialized enemies. Hence, structurally complex landscapes with high habitat connectivity may enhance the probability of pest regulation. In contrast, generalist and highly vagile enemies may even profit from the high primary productivity of crops at a landscape scale and their abundance may partly compensate for losses in enemy diversity. Conservation biological control also needs a multitrophic perspective. For example, entomopathogenic fungi, plant pathogens and endophytes as well as below- and above-ground microorganisms are known to influence pest-enemy interactions in ways that vary across spatiotemporal scales. Enemy distribution in agricultural landscapes is determined by beta diversity among patches. The diversity needed for conservation biological control may occur where patch heterogeneity at larger spatial scales is high. However, enemy communities in managed systems are more similar across space and time than those in natural systems, emphasizing the importance of natural habitat for a spillover of diverse enemies. According to the insurance hypothesis, species richness can buffer against spatiotemporal disturbances, thereby insuring functioning in changing environments. Seemingly redundant enemy species may become important under global change. Complex landscapes characterized by highly connected crop–noncrop mosaics may be best for long-term conservation biological control and sustainable crop production, but experimental evidence for detailed recommendations to design the composition and configuration of agricultural landscapes that maintain a diversity of generalist and specialist natural enemies is still needed.

Keywords: Agroecosystems; Beta diversity; Dispersal; Habitat fragmentation; Insurance hypothesis; Multitrophic interactions; Parasitoid and predator spillover; SLOSS; Spatial ecology; Specialists vs. generalists; Sustainability

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1. Introduction

Understanding conservation biological control requires a landscape perspective. Population dynamics and trophic interactions depend on processes at spatial scales larger

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than a single agricultural plot (Ricklefs and Schluter, 1993; Kareiva and Wennergren, 1995) and different species in a given area experience that area quite differently (Peterson et al., 1998). However, current ecological concepts often ignore the influence of spatial scale, in particular "the grey zone between the local mechanisms that are the traditional concern of community ecologists and the large scale processes that are the province of biographers and systematics" (Holt, 1993; see Leibold et al., 2004). In addition, pests and their enemies often bridge the crop–noncrop interface, demanding combined studies of both managed and natural systems (Altieri and Schmidt, 1986; Bianchi et al., 2006; Rand et al., 2006; Bommarco et al., in press).

In this paper, we identify a number of criteria to be considered for the sustainable management of biological control at different spatiotemporal scales, considering the relative roles of landscape composition and configuration and local agricultural intensification. These include crop–noncrop natural enemy spillover in relation to dispersal abilities and habitat specialization, metacommunity dynamics and the SLOSS debate, the multitrophic plant–fungus–insect context of biological control, predator beta diversity in human-dominated vs. natural landscapes and the insurance hypothesis. Finally, we conclude with recommendations for landscape planning to promote long-lasting conservation biological control.

2. Habitat fragmentation and crop vs. noncrop habitat in agricultural landscapes

The basis for conservation biological control lies in the fostering of natural enemies that are already present (Landis et al., 2000; Barbosa, 2003). During agricultural intensification, the overall complexity of the landscape is reduced, natural noncrop habitat is fragmented and the crop–noncrop landscape becomes a mosaic of relatively discrete habitat types (Daily et al., 2001; Tscharntke et al., 2002, 2005).

Habitat fragmentation is associated with low density of individuals of a given species and high rates of local and regional extinction, leading to low overall species diversity (Hanski, 1994; Harrison and Bruna, 1999; Tscharntke and Brandl, 2004). Individual habitat fragments may become too small to support particular species, and too far apart to be exploited in concert. Additionally, even if habitat fragments are large enough to support a species in the short term, they may be too far apart to ensure regional persistence through local extinction-colonization dynamics (Hanski, 1994; Hanski and Ovaskainen, 2000). Because resources become increasingly fragmented for higher trophic levels (Pimm and Lawton, 1977; Tscharntke et al., 2005b; van Nouhuys, 2005), natural enemies experience a sparser landscape than their phytophagous prey, the cost of which depends on their resource needs, behavior and phenology (Tscharntke and Kruess, 1999; van Nouhuys, 2005; Shaw, 2006; Elzinga et al., 2007). In an agricultural landscape, habitat fragmentation may be a greater problem for specialist parasitoids than for generalist predators, as the latter can use prey resources in a greater variety of habitat types (Golden and Crist, 1999; Tscharntke et al., 2005a,b; Rand and Tscharntke, 2007).

Agricultural landscapes range from structurally simple, dominated by arable crops, to structurally complex with high amounts of noncrop area (Fig. 1). Non-crop habitat types such as forest, hedgerows, field margins, fallows and meadows are temporally more stable and heterogeneous environments than (annual, arable) crops. They provide a number of important resources for parasitoids and predatory arthropods such as permanent vegetation cover suitable for over-wintering, refuges from disturbance, as well as resources such as alternative prey, pollen and nectar (reviews in Landis et al., 2000; Cronin and Reeve, 2005; Bianchi et al., 2006). Natural enemies contributing significantly to pest control must have a rapid numerical response to herbivore density. For this to occur, they must either be present in the cultivated habitat, be easily recruited from nearby, or colonize from a larger distance.

The crop habitat is generally more fertile than neighboring natural or near natural habitats, both due to non-random conversion of more fertile lands for agriculture, as well as the application of fertilizers and, in some cases, irrigation. Cropping systems often contain high prey resources at certain times of the year. On the other hand, agricultural habitats are characterized by disturbance and an increased risk of mortality due to crop management practices, such as pesticide application. Annual crops are, in addition, characterized by their limited suitability for over-wintering after harvest and subsequent tillage, and insufficient food resources such as nectar and pollen (Pfiffner and Luka, 2000; Holland and Reynolds, 2003; Thorbek and Bilde, 2004). Thus, the ephemerality, disturbance and high primary productivity of most agricultural landscapes are challenges to pest control by natural enemies (Wissinger, 1997; Landis et al., 2000; Tscharntke and Kruess, 1999).

3. Crop/non-crop natural enemy spillover, habitat specialization and dispersal ability

Habitat specialization is a popular characterization of the life-history strategy adopted by an organism. At two extremes lie species that are confined to either crop or to natural habitats (Duelli et al., 1990; Baldissera et al., 2004; Schmidt et al., 2007). Arthropods restricted to more natural habitats within the agricultural landscape mosaic have been termed "stenotypic species" (Duelli and Obrist, 2003). Such species (for example, carabid beetles restricted to woody habitat) are rarely found in crops. At the other end of the spectrum lie "cultural species" that have a strong preference for cultivated crops (i.e., occur in consistently higher abundances there), and generally do not depend on semi-natural habitats for their persistence within the landscape (Duelli and Obrist, 2003). A majority of agriculturally important arthropod natural enemies lie

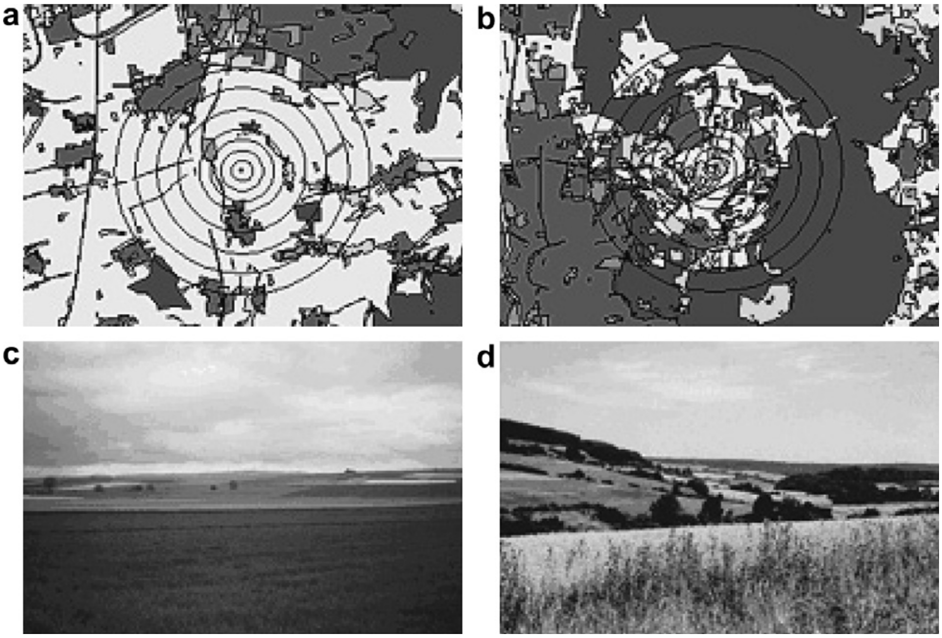

Fig. 1. Structurally simple (a and c) and complex (b and d) landscapes (near the city of Göttingen, Germany) showing the great contrasts in landscape composition with corresponding differences in natural-habitat fragmentation and landscape-wide species pools (see text for more details). (a–b) GIS data (white, arable crop area; the rest is noncrop area) with circles of different diameters indicating different and species-specific spatial scales experienced by the dispersing organisms. (c–d) Photos.

between these two extremes, requiring noncrop habitats to varying degrees (Landis et al., 2000; Duelli and Obrist, 2003; Bianchi et al., 2006), such that it is necessary for them to move between habitats to persist (Wissinger, 1997).

In agricultural landscape mosaics, natural enemies may move primarily from a particular habitat type to another, creating a source-sink dynamic (Pulliam, 1988). For example, some natural enemies may attack prey resources within crops, but are unable to sustain positive population growth within these habitats (Thies and Tscharntke, 1999; Bianchi et al., 2006). In this case their persistence within crop fields depends on a constant source of colonists from populations in surrounding non-crop habitats. For other natural enemies, movement is bi-directional, with individuals moving back and forth between crop and non-crop, depending on resource needs and availability. Both source-sink and bi-directional movement of natural enemies can result in spatial or temporal "spillover effects", in which resources available within one habitat type (e.g., alternative prey or overwintering sites in non-crop habitats) sustain enemy populations, and these enemies then spillover into another habitat type and exploit resources there (e.g., crop pests) (Landis et al., 2000; Rand et al., 2006).

Modeling studies suggest that "spillover" or "cross edge incursions" by generalist natural enemies from source habitats, where they receive resource subsidies, can substantially strengthen top-down control of prey species occurring within adjacent recipient habitats (Cantrell et al., 2001; Holt and Hochberg, 2001; Mouquet et al., 2005). The proximity of a near-natural habitat patch can thus result in increases in natural enemy abundance (Duelli et al., 1990; Dyer and Landis, 1997; Tscharntke et al., 1998), diversity (Clough et al., 2005), predator/prey ratios (Klein et al., 2002) and predation risk for crop pests (Thies and Tscharntke, 1999). Similarly, many species of natural enemies benefit from frequent movement between crop and noncrop habitats, even within a generation or growing season. For example, parasitoids and hover flies require herbivorous insects as hosts for their larvae, but feeding on floral resources as adults increases their longevity and potential fecundity. Field studies have demonstrated that external resource subsidies such as nectar can substantially enhance control of crop pests by such species (Tylianakis et al., 2004). For habitat generalists that use noncrop habitats, spatial and temporal patterns of resource use and dispersal will play a large role in determining their distribution and activity within crop fields, and the magnitude of natural enemy "spillover" into crops will depend greatly on the quality, quantity and proximity of noncrop habitat in the landscape (Cronin and Reeve, 2005; Bianchi et al., 2006). Spider diversity in agroecosystems, for example, may be the result of immigration from the surrounding species pool in noncrop habitats, while responses range from positive (19 species out of 40 tested) to negative (5 species). Depending on species, the spatial scales with the highest explanatory power for the arable spiders' density ranged from 95 m to 3 km radius around the study fields, potentially reflecting their dispersal distances (Schmidt et al., 2005, 2007, Fig. 2).

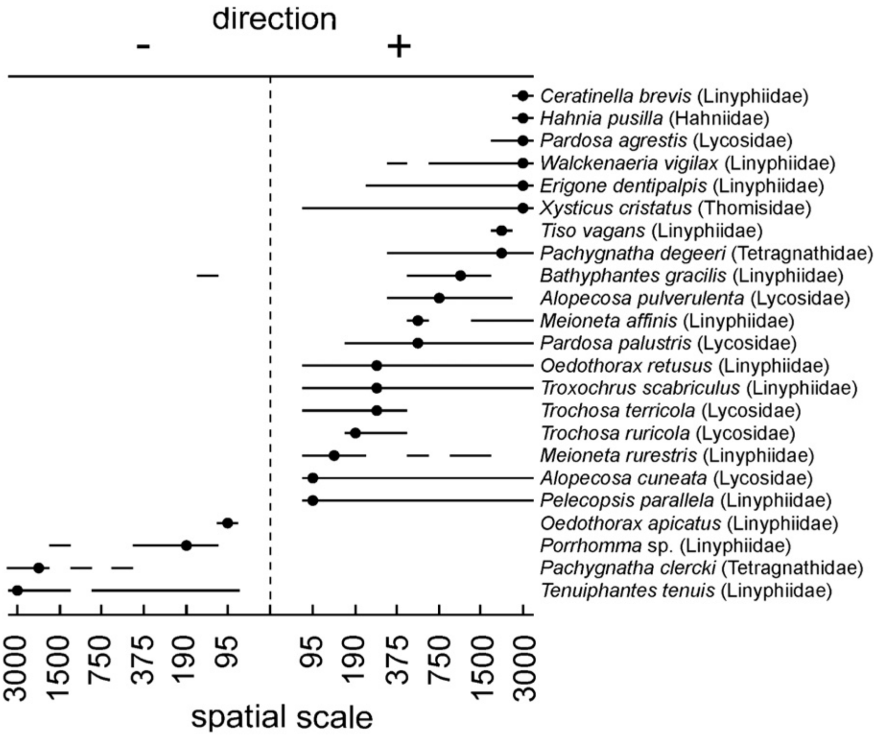

Fig. 2. Contrasting responses of arable spiders to the landscape matrix at different spatial scales (circles of different diameters, see Fig. 1). Direction and spatial scale of correlations between landscape composition (percent noncrop area in 38 human-dominated landscapes in Germany) and local densities of spider species are given. Negative correlations (spider density vs. noncrop habitat) are shown on the left side and positive correlations on the right side. Lines show the range of scales at which significant correlations to landscape composition were found. For each species, the spatial scale of the strongest correlation is marked with a dot. Data from Schmidt et al. (2007).

The scale at which crops and natural habitats are interspersed determines the degree of mobility necessary for spillover to play a significant role in the species composition in agricultural crops. Mobile natural enemy species should be favored in the colonization of agricultural crops. This has been found to be the case in a comparison of two spiders with different colonization abilities, where early colonization enabled one species to more effectively track resource abundance than the other within a 1-km^2 area (Marshall et al., 2000).

The importance of dispersal ability is sometimes demonstrated in the field as edge effects. For instance, there are many examples of parasitism rates or natural enemy abundances being higher at the edges of fields than in the middle (Altieri and Schmidt, 1986; Corbett and Rosenheim, 1996; Thies and Tscharntke, 1999; Nicholls et al., 2001; Tscharntke et al., 2002), suggesting limitation of dispersal distances from uncultivated area into fields. On the other hand, rates of parasitism are frequently found to be unrelated to distance from edge (as in Dyer and Landis, 1997; Tylianakis et al., 2004), suggesting that the number of natural enemies, rather than their movement, is limiting biological control. Very dispersive species may not exhibit edge effects, even if they do move into crops from natural habitats, but can still be sensitive to the large-scale landscape context. For example, ballooning spiders can be considered aerial plankton—the composition of which is determined to a large extent by the overall amount of noncrop habitat at large spatial scales (Schmidt and Tscharntke, 2005a,b; Clough et al., 2005). Many parasitoids have narrow host ranges (Shaw, 1994, 2006) and limited mobility (van Nouhuys, 2005), and may not have alternate hosts in surrounding uncultivated habitats. For these species, uncultivated habitat may provide nectar and shelter (Nicholls et al., 2000; Shaw, 2006), but potentially also hinder dispersal (Cronin, 2004; Vandermeer and Carvajal, 2001).

Habitat specialization and dispersion can be important determinants of natural-enemy impacts on herbivores in the crop–noncrop mosaic. However, much work remains to understand the long-term and landscape-wide dynamics. For example, while studies of immigration into crops are common (e.g., Landis et al., 2000), fewer have examined emigration of natural enemies from crops (Thomas and Jepson, 1999) and their effects on potential prey in noncrop habitats (see Rand et al., 2006, for a review of the existing literature). Theoretical approaches provide several predictions on predator–prey dynamics in complex landscapes (e.g., Holt and Barfield, 2003), but there are few empirical studies to support these predictions. Finally, while we know a great deal about patterns of natural enemy distribution and diversity in crop fields in relation to non-crop habitat, we still lack information on how such patterns influence suppression of crop pests.

4. Metapopulation and metacommunity ecology in agricultural landscapes

When a collection of habitat patches are occupied by individuals that occasionally disperse among them, metapopulation processes may allow regional persistence of a species that would not persist on a local scale (reviewed in Hanski, 1994). Early metapopulation theory was in fact developed by Levins (1969) to address an agricultural question: should the control of a pest use synchronous or asynchronous applications of pesticides over a large spatial area? He concluded that simultaneous local extinctions caused by synchronous control would cause greater overall reduction in pest density than asynchronous control that left local refuge populations of potential migrant pests.

For classical biological control, configuration of the cultivated land should allow specific natural enemy species to persist, respond numerically to host density and move through the matrix among crop patches (Ives and Settle, 1997; Kean and Barlow, 2001). Single species metapopulation theory does not predict successful classical biological control (Kean and Barlow, 2000) because such an effective natural enemy would be unlikely to act synchronously over a large area (Hawkins et al., 1999), and without a host refuge the natural enemy would not persist (see Reeve and Murdoch, 1986; Ives and Settle, 1997).

Conservation biological control does not depend on particular species of natural enemies with population dynamics tightly linked with those of the host or prey. If an unspecialized natural enemy community were distributed over a landscape, then perhaps the synchronized pest suppression (though not elimination) postulated by Levins (1969) would occur at least to some extent. Because conservation biological control depends on a community of natural enemies—not a single natural enemy species—their dynamics in crop and noncrop areas should actually be considered in the context of metacommunities (Leibold et al., 2004). In some cropping systems, it may even be realistic to think of the host and the natural enemies communities as separate, with the hosts primarily inhabiting the ephemeral resource rich crop patches, and the natural enemies mainly inhabiting uncultivated patches in a cultivated matrix.

Much metacommunity theory has developed over the last few years, some focusing on non-equilibrium communities, and assembly rules (Holyoak et al., 2005). This theory has yet to be used for agricultural landscapes, and should be particularly applicable for making predictions about the effectiveness of conservation biological control. For conservation biological control, we are concerned with enhancing abundance and diversity of natural enemies so we should therefore also look at the field of conservation ecology for new approaches (Tscharntke et al., 2002, 2005). Conservation ecologists design reserves to facilitate the growth or stability of populations of a single species, or to a lesser extent the diversity of particular communities. Because land, financial and social resources are considered limited, there is debate about the quality, size, shape, and connectivity of habitat fragments necessary to set aside for conservation (Cabeza and Moilanen, 2001; Van Teeffelen et al., 2006). This considerable body of research can be applied with some modification to conservation biological control. For instance, a long-standing question is whether land set aside for reserves should be concentrated into a single large fragment or distributed as several smaller fragments (the SLOSS debate) (May, 1975; Simberloff and Abele, 1976). For a single species, regional (metapopulation) persistence in the face of environmental variability favors several small patches, whereas overall population size might be largest in a single large patch (Ovaskainen, 2002; Tscharntke et al., 2002). For an entire community, species richness increases with habitat area, so a larger block of habitat should support more species than small ones (May, 1975; Simberloff and Abele, 1976). Conversely, if each small patch supports a different species composition, then the total number of species could be greater than would co-exist in one large habitat patch (see the beta diversity section below; Simberloff and Abele, 1976; Tscharntke et al., 2002; Leibold et al., 2004).

A large uncultivated area may be a good source of natural enemies, but its utility would depend on the dispersal abilities of different insect species into the surrounding cultivated area. Alternatively, if the uncultivated source area were distributed in smaller fragments among cultivated fields then dispersal limitation would be reduced, but fewer individuals and species of natural enemies would be available. Hence, when the amount of uncultivated land is limited there may be a tradeoff between connectivity of noncrop habitat and natural enemy diversity and population size.

The appropriate configuration of noncrop habitat also depends on attributes of the crop and the pests. For ephemeral annual crops, widely distributed small, noncrop areas may facilitate natural enemies moving quickly into the crop (Bianchi et al., 2006). For perennial crops, perhaps a single large refuge harboring a diverse natural enemy community might be desirable. Accordingly, extremely mobile pests, or pests with high reproductive rates may be controlled more effectively by natural enemies where there is high connectivity of the uncultivated habitat.

Over the last few years, conservation biologists have been developing complex algorithms to design nature reserves taking into account the importance of cost, diversity, connectivity, stability, and population sizes (Arponen et al., 2005; Cabeza and Moilanen, 2001). These programs have been used for practical applications (Moilanen et al., 2005), and could undoubtedly be modified for the design of agricultural landscapes, and to evaluate existing landscapes, exploring potential modifications.

5. Multitrophic plant-fungus-insect context of biological control

Microorganisms interact with natural enemies and their responses to pests and landscape features. The seasonal dynamics of natural–enemy dispersal across the crop–noncrop interface may be strongly influenced by several fungal pathogens. In this section, we review the relationship between landscape structure and the biological control of pest organisms within a multitrophic context, although empirical research dealing with these issues is rather scattered and far from giving a comprehensive understanding. We postulate that (i) population regulation of aphids by predators, parasitoids and/or entomopathogenic fungi is a multitrophic-level process, (ii) plant pathogens add heterogeneity to herbivore-natural enemy-interactions, and (iii) below- and above-ground microorganisms interact to influence the outcome of biological control. The microorganisms, herbivores, and natural enemies involved in such multitrophic-level interactions likely respond to landscape heterogeneity at very different spatial scales (van Nouhuys and Hanski, 2002; Hedlund et al., 2004; Tscharntke et al., 2005b).

Interactions between invertebrate hosts and their entomopathogenic fungi may be regarded as an arms race with co-adaptations resulting in behavioral changes (Roy et al., 2006), such as changing feeding site preferences of aphids (Roy et al., 2002; Jensen et al., 2001), aphids leaving host plants more frequently (Jensen et al., 2001) and responding less sensitively to alarm pheromones produced by aphids (Roy et al., 1999). Further, herbivores may suffer from reduced predation (Pell et al., 1997; Roy et al., 1998), while some aphid parasitoids may not alter their behavior until the entomopathogen kills their aphid hosts (Brobyn et al., 1988; see also Table 1 and Fig. 3). Host plants and timing also influence the outcome of these interspecific interactions (Fuentes-Contreras et al., 1998).

Recent evidence suggests that landscape factors contribute to the dynamics of pest insect–pathogen interactions. Dispersal of entomopathogenic fungi of aphids is at least partly related to the migratory flight of alatae (Feng et al., 2004, 2007). Aphid clones differ in their susceptibility to isolates of entomopathogens or to parasitoid species (Ferrari and Godfray, 2006), and the exchange of specific aphid clones between crop and noncrop habitats appears to be limited (Vialatte et al., 2005). Dispersal processes of aphids between crop and noncrop habitats at a local scale were studied recently. Vialatte et al. (2006) traced individual movements of cereal aphids (*Sitobion avenae* Fbr.) and found distinct source-sink dynamics between aphids in wheat and maize fields. However, whether and how these dispersal processed are linked to the surrounding habitat composition needs to be studied in detail. Several factors may influence source-sink dynamics, including the roles of host range of entomopathogenic fungi, movement and transmission of infected hosts, and refugia of aphid epizootics (Steinkraus, 2006). A reservoir of entomopathogenic fungi in noncrop aphids may result in higher infection rates of aphids in crop plants when predators spillover from noncrop to crop (Ekesi et al., 2005).

Other insect–fungus interactions may also play a role in biological control. A recent study on a bethyliid parasitoid, introduced from Africa to many coffee-producing countries to control the coffee-berry borer, highlights a much more intricate interaction between biological control options and microorganisms. This parasitoid species has been shown regularly to carry a mycotoxin producing fungus (*Aspergillus westerdijkiae* Frisvad & Samson) (Vega et al., 2006). This fungus produces ochratoxin A, which occurs in many agricultural commodities and is well known to be a human toxin. This finding has important implications for valuation of biological control management, because parasitoids spreading a toxin-producing fungus over large areas counteract the potential benefits of pest control. The maintenance of a high fungal spore load on dispersing individuals may be enhanced by alternative resource use in the absence of the main host and point to the need for studies integrating different spatiotemporal scales.

Plants are attacked simultaneously by a suite of microorganisms, including pathogenic or endophytic fungi, and herbivores (e.g., Biere et al., 2002; Cardoza et al., 2003a,b), and these species as well as their enemies are probably differently affected by the surrounding landscape. Herbivore-induced plant volatiles are known to play a major role in host finding by parasitic wasps (DeMoraes et al., 1998; Dicke and van Loon, 2000). Plants that are colonized by pathogenic fungi may produce volatiles different from the bouquet released when attacked by a herbivore alone, which may affect their attractiveness to parasitoids. This might have a landscape scale effect because infections of plants by fungal pathogens are generally patchy (Burdon et al., 1989; Laine, 2004; Laine and Hanski, 2006). More detailed studies are needed to evaluate the potential impact of the pathogen-added heterogeneity to biological control options. Plant-pathogen dynamics can operate on a large spatial scale and may be influenced by insect vectors (Kluth et al., 2002; Thrall et al., 2003; Laine and Hanski, 2006). We therefore need to understand how disease epidemiologies influence resource exploitation patterns in natural enemies searching for their hosts in agroecosystems. Cropping patterns and noncrop refugia influence eradication and decolonization processes operating on distinctly different spatiotemporal scales.

Below-ground processes also influence above-ground interactions (Wardle and van der Putten, 2002; see Table 1 and Fig. 3). Mycorrhizal fungi are associated with most crop plants, but their prevalence varies with agronomic measures (Douds et al., 1995; Kabir, 2005). Thus, cropping patterns *per se* add heterogeneity to these processes. Mycorrhizal fungi affect the performance of above-ground herbivores, either increasing (Gange et al., 1999; Goverde et al., 2000) or decreasing (Gange et al., 1994; Gange and Nice, 1997) their survival and abundance. The importance of these below-ground processes for above-ground food webs has been demonstrated by Gange et al. (2003), showing that parasitism rates by a eulophid wasp parasitizing an agromyzid fly were reduced in greenhouse experiments when plants were inoculated with specific arbuscular mycorrhizae (AM-fungi). However, the effects on the para-

Table 1
Multitrophic plant-fungus-insect context of biological control

Herbivorous insect or natural enemy	Microorganisms	Crop/host plant or host insect	Interactions	Interaction No.	Reference
Aphids (*Sitobion avenae* Fbr., *Acyrthosiphon pisum* Har.)	Entomopathogenic fungus (**EF**) (*Pandora neoaphidis* (Remaudière and Hennebert))	Wheat, Lucerne	**EF** altered feeding behaviour of aphid	1, 3	Jensen et al. (2001); Roy et al. (2002)
Aphid (*Acyrthosiphon pisum* Har.)	**EF** (*Pandora neoaphidis* (Remaudière and Hennebert))	Faba bean	**EF** reduced response to alarm pheromone in aphid	1, 2	Roy et al. (1999)
Coccinella septempunctata L.	**EF** (*Pandora neoaphidis* (Remaudière and Hennebert))	*Acyrthosiphon pisum* Har.	Predator exhibited preference for non-infected vs. infected aphids	1, 2, 6	Pell et al. (1997); Roy et al. (1998)
Parasitoid (*Encarsia formosa* Gahan)	**EF** (*Aschersonia aleyrodis* Webber)	Whitefly (*Trialeurodes vaporariorum* West.)/Tomatoes	Whiteflies less parasitized when infected by the **EF**	1, 2, 6	Fransen and van Lenteren (1993)
Parasitoid (*Aphidius ervii* Hal.)	**EF** (*Pandora neoaphidis* (Remaudière and Hennebert))	Faba bean	Non influence of **EF** on foraging behaviour	1, 2, 6	Baverstock et al. (2005)
Parasitoid (*Aphidius rhopalosiphi* DeStefani-Peres)	**EF** (*Pandora neoaphidis* (Remaudière and Hennebert))	Aphid (*Metopolophium dirhodum* (Walker))	Influence of **EF** on parasitism rate only at late infection stage of hosts	1, 2, 6	Brobyn et al. (1988)
Green peach aphid (*Myzus persicae* (Sulz.))	EFs	Potatoes	Higher populations—fungicide treatments probably reduced **EF**s	1, 10	Nanne and Radcliffe (1971)
Coccinella septempunctata L.	**EF** (*Pandora neoaphidis* (Remaudière and Hennebert))	Various aphid species	Presence of coccinellids enhanced infection of aphids by **EF**s	1, 2, 6	Ekesi et al. (2005)
Aphid (*Sitobion avenae* Fbr.) Parasitoid *Aphidius rhopalosiphi* DeStefani-Peres	**EF** (*Pandora neoaphidis* (Remaudière and Hennebert))	Resistant/ susceptible wheat cultivars	Competitive outcome of interactions depending on timing	1, 2, 3, 5, 6	Fuentes-Contreras et al. (1998)
Aphids	EFs		Dispersing aphids also disperse **EF**s and parasitoid larvae	1, 5, 10?	Feng et al. (2004, 2007)
Mustard leaf beetle (*Phaedon cochleariae* Fbr.)	**EF** (*Metarhizium anisopliae* (Metsch.))/plant pathogen (*Alternaria brassicae* Berk)	Chinese cabbage	Higher mortality of larvae fed with pathogen infected leaves	3, 10	Rostas and Hilker (2003)
Parasitoid (*Prorops nasuta* Waterston)	Mycotoxin producing fungus (*Aspergillus westerdijkiae* Frisvad & Samson)	Coffee	Biocontrol agent might be able to disseminate human toxic fungus	2, 8	Vega et al. (2006)
Aphids	Endophytic fungus	Grasses	Reduced parasitism rates in aphids feeding on endophyte infected plants	8, 9, 10	Omacini et al. (2001)
Noctuid moth (*Hadena bicruris* Hufn.)	Plant pathogen (*Microbotryum violaceum* (Pers.))	*Silene latifolia* Poiret	Higher larval mortality on infected plants due to higher parasitism rates (reduced enemy free space)	3, 9, 10	Biere et al. (2002)
Beet armyworm (*Spodoptera exigua* Hbn.)	Plant pathogen (*Sclerotium rolfsii* (Sacc.))	Groundnut (=Peanut)	Parasitoid showed preference towards pathogen infected plants	8, 9, 10	Cardoza et al. (2003b)
Agromyzid (*Chromatomyia syngenesiae* Hardy)	Arbuscular mycorrhizae (**AM**)	*Leucanthemum vulgare* Lam.	Parasitism rate reduced on **AM** colonized plants	2, 4, 11, 13	Gange et al. (2003)
Common blue butterfly (*Polyommatus icarus* (Rot.))	Arbuscular mycorrhizae	*Lotus corniculatus* L.	Increased larval weight on plants colonized by **AM** fungi	3, 4, 11	Goverde et al. (2000)
Black vine weevil (*Otiorhynchus sulcatus* (Fbr.))	Arbuscular mycorrhizae	*Taraxacum officinale* Veb.	Decreased survival of larvae on **AM** colonized plants	3, 4, 11	Gange et al. (1994)
Mexican bean beetle (*Epilachna varivestis* Mulsant)	Arbuscular mycorrhizae	Soybean	Improved fitness of beetles reared on moderately stressed **AM** host plants	3, 4, 11	Borowicz (1997)
Plant Pathogens	Arbuscular mycorrhizae	Diverse	Reduced disease incidence on **AM** colonized host plants	8, 10, 12	Azcón-Aguilar and Barea (1997)

Interaction types are numbered and referred to in Fig. 3.

sitoid were mycorrhizal species-dependent. We are not aware of any studies on the impact of below-ground colonizing AM-fungi on above-ground pest–enemy interactions and biological control success.

The few examples cited above are in favor of a multitrophic approach for biological control at a landscape level, including processes modified by below-ground and above-ground microorganisms (Vicari et al., 2002), induced

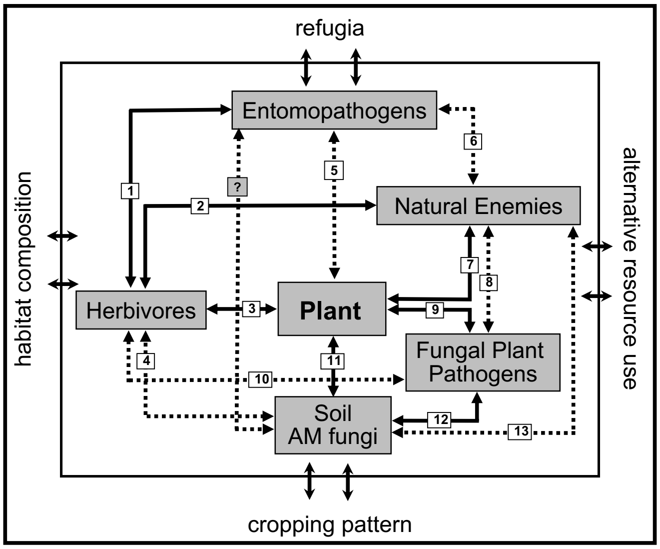

Fig. 3. Conceptual framework showing how direct (solid lines) and indirect (dashes lines) interactions mediate pest regulation within and between habitats. Numbers on arrows refer to examples and citations of Table 1. Question mark indicates possible interactions which have not been documented so far. AM, arbuscular mycorrhizae.

responses in plants (Stout et al., 2006), and spatially different colonization abilities of microorganisms, natural enemies, and herbivores.

6. Natural enemy beta diversity at different spatiotemporal scales

Beta diversity is a measure of the diversity among local communities. It is the outcome of spatial and temporal heterogeneity in species distributions that may result from habitat heterogeneity, dispersal limitation, or chance effects (Crist and Veech, 2006). It is not surprising that spatial beta diversity is generally higher within natural, more heterogeneous habitats than within modified agricultural systems (Tylianakis et al., 2005, 2006a). For example, the beta diversity of plants is lower among samples within fields that are intensively managed than in extensively managed farms or semi-natural habitats (Wagner et al., 2000; Roschewitz et al., 2005). Among fields or natural habitat patches, however, beta diversity may be considerably higher, depending on differences in management intensity or habitat heterogeneity (Wagner et al., 2000; Roschewitz et al., 2005; Tylianakis et al. 2005, 2006a; Crist and Veech, 2006).

The connectivity of different habitats or land-use types may influence species movements with low patch connectivity leading to higher beta diversity because of local extinction and dispersal limitation, or because stochastic colonization from the regional species pool results in different subsets of species occupying isolated patches (see Leibold et al., 2004). Diekötter et al. (in press) found greater levels of beta diversity among patches of natural and semi-natural habitats with less connectivity than among patches that were more highly connected in different agricultural landscapes in Switzerland. In a mosaic agricultural landscape, therefore, the turnover of species among patches, or 'beta diversity', can contribute significantly to the overall arthropod diversity of the region (Gering et al., 2003; Summerville et al., 2003; Tylianakis et al., 2005, 2006a).

Species turnover through time can also be greater in unmodified habitats than in intensively managed agricultural systems (Tylianakis et al., 2005), indicating that natural habitats are more heterogeneous in both space and time. This may be because some species move in and out of natural habitats, using crops when resources there are available (Wissinger, 1997). An alternative explanation is the species-area-time relationship. Sampling mobile species over a longer period increases the time available for them to cross larger distances and enter the sampling area (trap). Therefore, long-term sampling effectively samples a greater area of the habitat (Ulrich, 2006), thereby including more microhabitat types in long-term samples from heterogeneous systems. In this sense, beta diversity in time may be intrinsically linked to beta diversity in space, and both will increase with increasing habitat heterogeneity.

At regional scales, greater levels of beta diversity are expected to occur across landscape mosaics. Patches of similar habitat separated by large distances (10–100 km) may have different admixtures of species because of local sampling of the regional species pool and limited movements of species between habitats (Nekola and White, 1999; Qian et al., 2005). This distance-dependent similarity in species composition is a common pattern in natural communities (Resetarits et al., 2005), and may be especially important in agricultural landscapes with isolated natural and semi-natural habitats. Here, we expect that both habitat heterogeneity and patch isolation will have important effects on turnover of species in natural and semi-natural habitats surrounding agricultural areas.

Cross-edge spillover of natural enemies from adjacent natural fragments into agricultural fields (see above and Rand et al., 2006) may depend strongly on the local species available in adjacent patches. If beta diversity is high, then each local assemblage may comprise a small fraction of the overall regional pool of species, and the set of species moving across habitat boundaries may vary from place to place. This is exemplified by a study that recorded beetle richness and abundance along habitat edges, between cornfields and adjacent forest patches, in eight different locations within a 50-km^2 area of an agricultural landscape in Ohio, USA (Dudziak and Crist, unpublished). The species richness of predatory beetles was consistently highest along corn-forest boundaries, where spillover occurred between habitats (Fig. 4a). Beta diversity among habitats (corn, edge, forest) was significantly higher than expected by chance (sample-based randomization; Crist et al., 2003) because of the high degree of species turnover along habitat boundaries. As a proportion of the total sampled richness, however, among-habitat diversity along transects is relatively small compared to the beta diversity among the eight sites where different field-forest boundaries were sampled (Fig. 4b). High levels of among-site beta diversity suggest that a different pool of predatory beetles occurs in natural habitats adjacent to corn fields in different parts of the landscape (Fig. 4).

Beta diversity among patches can contribute significantly to the total diversity of agricultural landscapes. If biodiversity promotes ecosystem functioning in predator–prey or parasitoid host systems at larger spatial scales (Tylianakis et al., 2006b; Snyder et al., 2006, Straub et al., this issue), high regional diversity resulting from high beta diversity may carry benefits for biological control (see Fig. 5). Further, species that do not contribute to biological control in one patch may be important in other patches (Srivastava and Vellend, 2005), providing spatial “insurance” (Loreau et al., 2003) in pest control. For example, if different natural enemy species have different microhabitat preferences or abilities to use prey at different densities (e.g., Tscharntke, 1992; Tylianakis et al., 2006b), high beta diversity may allow efficient exploitation of heterogeneous pest populations or pest populations at different densities. Between-patch species turnover may both promote regional diversity that enhances ecosystem functioning (Srivastava and Vellend, 2005) and provide a variety of different functions at the regional scale (Bond and Chase, 2002). The importance of consumer beta diversity for rates of consumption has not yet been shown in practice, however, and further investigation is needed on the relative effects of high alpha (average sample) vs. beta (between sample turnover) diversity on rates of predation or parasitism. Indeed, one study showed that high temporal beta diversity was less important in maintaining stability of parasitism rates than was a high temporal variation in alpha diversity (Tylianakis et al., 2006b). Irrespective of whether high beta diversity leads to increased mean attack rates on pest arthropods, one of the greatest potential benefits of maintaining beta diversity may be as insurance in variable environments (see below).

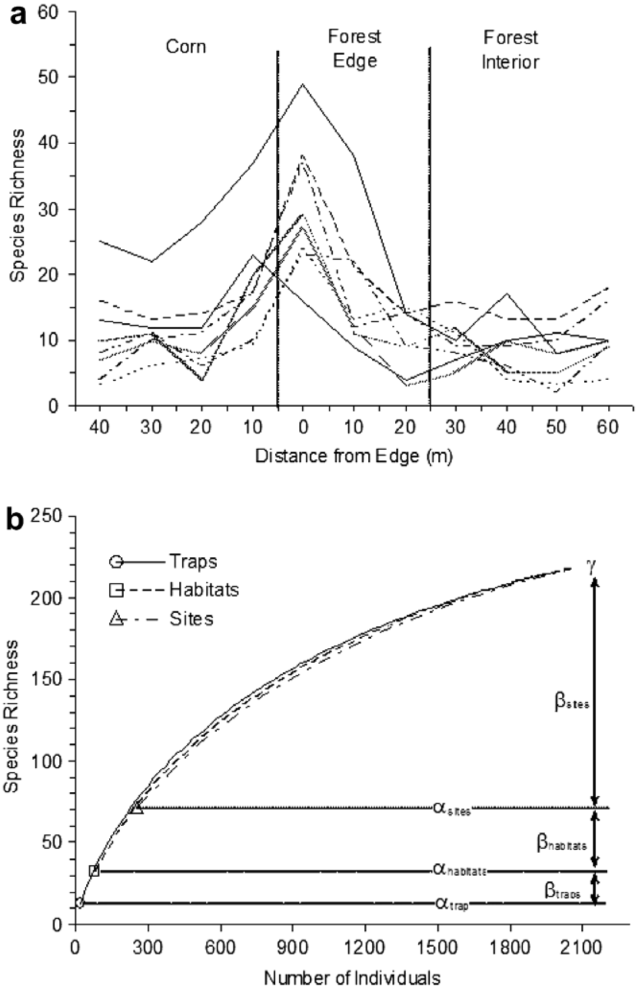

Fig. 4. Species richness of predatory beetles sampled in traps at 10-m intervals along transects spanning corn and forest habitat. (a) Patterns of species richness shown by eight transects from different locations. (b) Additive partitioning of the rarefaction curve of species richness (see Crist and Veech 2006) of predatory beetles, in which total species richness (gamma) is decomposed into the species richness within traps ($\text{alpha}_{\text{trap}}$), among traps ($\text{beta}_{\text{trap}}$), among habitats ($\text{beta}_{\text{habitats}}$), and among sites ($\text{beta}_{\text{sites}}$). Most of the beta diversity is due differences in species composition among fields located in different parts of the landscape.

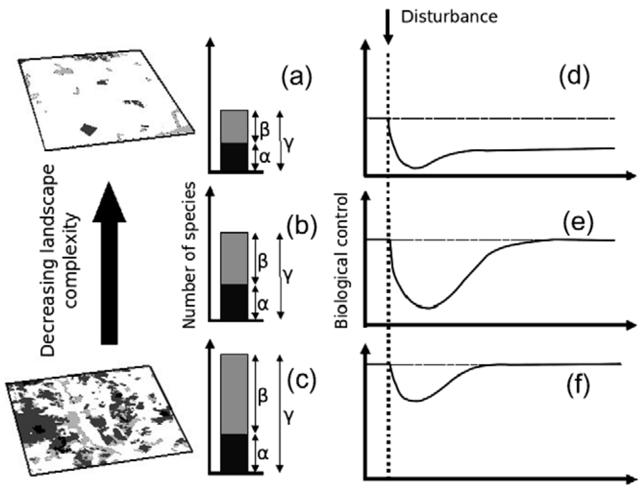

Fig. 5. Hypothesized response to disturbance on biological control by native natural enemies (conservation biological control) in different landscapes, showing how beta diversity (a–c) and recover of biological control after disturbance (d–f) change with landscape heterogeneity. (a and d) Intensely used monotonous landscape with a small available species pool, giving a low general level of biological control, a greater dip in biological control after a disturbance and an ecosystem that is unable to recover. (b and e) Intermediate landscape harbouring slightly higher species richness, rendering deeper dip and slower return from a somewhat lower maximum level of biological control after a disturbance. (c and f) Heterogeneous landscape with large species richness, mainly due to the higher beta diversity, rendering high maximum level of biological control, and low dip and quick return in biological control after a disturbance. Modified after Bengtsson et al. (2003).

7. The insurance hypothesis—enemy richness in mosaic landscapes

The insurance hypothesis (Yachi and Loreau, 1999) purports that species richness can buffer against fluctuations in ecosystem functioning, thereby insuring function in fluctuating environments. In environments with high species diversity, there is a greater probability that seemingly redundant species can become important in the maintenance of biological control in certain situations, e.g., following disturbance (Ives and Cardinale, 2004). This is especially important in crop systems, where temporal fluctuations in resource availability, caused by sowing and harvest, can drive between-patch fluxes of predatory arthropods (Rand et al., 2006). If natural enemy populations in a particular crop require time to build up their population size, populations of different enemies in adjacent habitats may provide spatiotemporal complementarity, preventing early pest outbreaks (Bianchi et al., 2006). Under predicted global change scenarios, climatic variation is expected to increase (www.ipcc.ch), and high diversity of species at the landscape scale may be essential for maintaining ecosystem functions such as biological control.

A prerequisite for insurance is that species differ in their response to a changing environment, for example by reacting differently to variable resource levels or abiotic parameters (Elmqvist et al., 2003). These ideas are largely derived from theory using statistical relationships such as the portfolio effect (Doak et al., 1998), and more complex models including multiple resource competition and dominance (Tilman, 1999). Stringent empirical tests of this hypothesis are, however, largely lacking. Some studies, although fraught with problems (Loreau et al., 2002), support the idea that stability and predictability of ecosystem functioning is promoted by higher species diversity. Data are mostly from grassland communities (McNaughton, 1977, 1985; Tilman, 1999) and microbial communities (Naeem and Li, 1997; McGrady-Steed et al., 1997) and generally deal with biomass productivity or decomposition (but see Tylianakis et al., 2006b).

A major problem is scaling up these results from plot-level experiments to biological control exerted by a community of natural enemies in agricultural landscapes. Disturbances and environmental variation act at several spatial and temporal scales and such scale-dependent effects on biological control are often ignored in agroecosystems (Bengtsson et al., 2003). Current land use and environmental changes affect ecosystem functions at broad scales (Srivastava and Vellend, 2005) and disturbances at these levels require a landscape-level species pool from which to draw new species for buffering the ecosystem service (Bengtsson et al., 2002, Fig. 5). In its original form, the insurance hypothesis emphasizes local effects on species survival. Insured ecosystem functionality is, however, also linked to the spatial setting of the environment, where recovery after a disturbance is contingent on the access of a landscape level species pool, and where dispersal and exchange of species among landscape elements and landscape structure ensures recolonization (Loreau et al., 2003; Bengtsson et al., 2003). This is particularly relevant for conservation biological control and native predators where access to crop and noncrop habitats is key for the maintenance of a diverse and abundant predator community (Tscharntke et al., 2005a,b; Bianchi et al., 2006). Therefore, we need to understand how both local and landscape level processes affect long-term stability and resilience of biological control by native predators.

The research on long-term and large-scale relationships between predator richness and biological control is still in its infancy. We need a better understanding of how species diversity and landscape composition affects the long-term stability and resilience of biological control. Specifically, we recommend: (1) the assessment of the spatio-temporal variability of predation in controlled experiments at different natural enemy diversities and landscape types; (2) studies of long-term predator community dynamics and species turnover, combined with studies on the population dynamics of dominant natural enemy species; and (3) measurements on the delivery of the ecosystem function, *i.e.,* predation efficiency and pest suppression in these multiple locations and over time.

The link between predator species richness and pest suppression, and the extent to which different predator species contribute to pest suppression, has been addressed in a number of recent experiments. The outcome is variable. Higher predator species richness may weaken (Rosenheim et al., 1993; Snyder and Wise, 2001; Finke and Denno, 2004), strengthen (Losey and Denno, 1998; Snyder and Ives, 2003; Schmidt et al., 2003; Wilby et al., 2005; Snyder et al., 2006) or have neutral (Chang, 1996; Wilby et al., 2005; Straub and Snyder, 2006) effects on herbivore suppression. Problems with these experiments are that they use a maximum of four species, often less. Although some studies consider diversity of species groups or taxa (Snyder and Wise, 2001; Snyder and Ives, 2003; Schmidt et al., 2003), these results make it difficult to test predictions of the biodiversity - ecosystem function outcome in natural, more species rich communities (Kremen, 2005) and in particular when considering the heterogeneity of a landscape scale. A general conclusion of these experiments is that species identity is crucial for the outcome (Cardinale et al., 2006). Variability may therefore reflect the idiosyncrasy that can be expected for the ecosystem function at low species richness, and that a higher diversity is needed to reach stable and predictable pest suppression (Doak et al., 1998). Another important conclusion is that the complexities of predator intra-guild interactions cannot be disregarded when developing conservation biological control schemes (Prasad and Snyder, 2006).

The composition of the predator community in relation to agroecosystem management and landscape structure are important pieces of information for understanding how diversity may affect long-term stability and resilience (see Duelli and Obrist, 2003; Öberg et al., 2007). There are strong indications that a mosaic landscape harbors a larger number of species for several taxa, among them predators (reviewed in Tscharntke et al., 2005b; Bianchi et al., 2006), and that farming practices with low or no pesticide input have a positive effect on predator diversity (Bengtsson et al., 2005). The predator community in the agricultural ecosystem is generally dominated by a few species only. For instance, intensive sampling of lycosid spiders in Swedish agricultural fields and grassy field margins resulted in a species richness of 18 species. Of these, one species accounted for 57% and three species accounted for 92% of the overall abundance (Öberg et al., 2007). In the same study 47 linyphiid spider species were found. Three of these species accounted for 88% of the abundance (Öberg et al., 2007). A similar pattern has been found for other predator groups such as ground beetles (Ekbom-Sohm and Wiktelius, 1985), and parasitoids (Menalled et al., 2003; Tylianakis et al., 2007). These dominance patterns need to be considered if we are to understand the effect of species diversity on the stability of biological control.

We can consider the extreme case where dominance patterns are constant over time and similar in several locations. This implies that diversity, *per se*, is less important for ensuring a stable ecosystem function (although diversity could still increase the magnitude of the function). In this case we would focus on enhancing the abundance of common predators identified as efficient control agents. If, on the other hand species turnover is high, we expect species diversity to be important for ensuring reliable pest suppression in the short as well as the long term. Few studies specifically address temporal variation in predator species turnover and dominance patterns in agricultural ecosystems. There are, however, studies that show a large turnover within and between years for important predator groups such as parasitoids (Tylianakis et al., 2005; Menalled et al., 2003; Thies et al., 2005), and coccinellids (Elliott et al., 2002; Bommarco, unpublished). Long-term studies on temporal community dynamics of generalist predators are scant. Many years of sampling of carabids in Europe have demonstrated decreased diversity and reversed dominance patterns over time (Desender and Turin, 1989; Holland, 2002). Part of this change in diversity is likely to be a result of changing farming practice, with increased pesticide use and decreased landscape heterogeneity over time. Therefore, it is difficult to discern the variation in predator communities that would be expected when farming practice and landscape structure is held constant.

There are several studies showing that the species richness and abundance of predators is strongly affected by both landscape heterogeneity and farming practice (Holland, 2002; Cronin and Reeve, 2005; Bengtsson et al., 2005; Schmidt and Tscharntke, 2005a,b; Schmidt et al., 2005; Bianchi et al., 2006; Öberg et al., 2007). Less is understood about how landscape and management practice affects the variability of the predator community and thereby the stability of ecosystem functions. In one available study, higher land use intensity led to higher species turnover and a lower mean diversity for parasitoids, and a less stable ecosystem function (parasitism rate) (Tylianakis et al., 2006b). More information is obviously needed on predator community dynamics and changing food web interactions over time and space, and how that is affected by management practice and landscape structure (see Tylianakis et al., 2007). A possible working hypothesis is that diversity is higher and community composition is more variable in complex landscapes with low-intensity land use, and that the stability, predictability and magnitude of the pest suppression is lower in intensively used, simple landscapes (Fig. 5a and d) compared to more complex landscapes (Fig. 5c and f).

We cannot, at this point, conclude that the insurance hypothesis is correct. However, we know that predator abundance and diversity largely depends on landscape structure and farming practice in agricultural ecosystems. There are good reasons to believe from theory, but also from the bits and pieces of empirical results, that maintaining diversity is important to safeguard a long-term stable delivery of biological control from native predators. Here we have placed emphasis on the ability of the system to return to a certain level of biological control after a disturbance. The insurance idea has ultimately to be extended to include the possibility of non-reversible effects (Elmqvist et al., 2003; Fig. 5d), something that should further increase our risk awareness in our use of the natural resources.

8. Recommendations for sustainable landscape planning

How can we sustainably conserve rich arthropod communities and the biological control services they provide? This review provides evidence that the conservation of arthropods and the enhancement of biological control need a landscape perspective and the consideration of possible interacting effects of landscape context and local habitat quality (Tscharntke et al., 2005b; Kleijn and van Langevelde, 2006). Assessments based solely on the diversity of local plots may lead to an overestimation of sustainable biological control, because local diversity will be comprised of a few common species with unknown performance in the future. In addition, enemy communities in managed systems tend to be similar, thereby reducing beta diversity on a landscape scale, further reducing the conservation value of agroecosystems (Tylianakis et al., 2005). Possible benefits of local, field-scale measures to enhance arthropod diversity or biological control therefore depend on the composition and configuration of the surrounding matrix (Tscharntke et al., 2005b). For example, local (farm-scale) practices often enhance the density of a few key species, whereas species richness is contingent on landscape scale complexity (Roschewitz et al., 2005; Schmidt et al., 2005, 2007; see Fig. 2). Hence, local management may promote biological control with common species, but neglects the role of arthropod diversity. Even in the most intensively farmed landscapes it is usually possible to enhance diversity and abundance of the most common generalist species of arthropods, whereas more uncommon, specialist species are often missing (Kleijn et al., 2001, 2006). This may result in substantial biological control benefits where biological control is correlated with just the abundance of a common biocontrol agent, but not in situations where high species richness of natural enemies causes a high mortality of hosts or prey (Snyder et al., 2006; Tylianakis et al., 2006b). The insurance hypothesis states that high diversity within a functional group is needed to guarantee this function in an ever changing world. Current initiatives to enhance biological diversity and associated ecosystem services on farmland, such as the European agri-environment schemes, focus on local management at a farm level, whereas only the consideration of the landscape context will ensure sustainable biological control that is based on rich enemy communities and their capacity to reorganize after disturbances (Tscharntke et al., 2005b; Bianchi et al., 2006).

Agricultural intensification at a landscape scale makes promotion of locally rare or uncommon natural enemies a difficult task, first because few of these species are found on farmland (Kleijn et al., 2006), and second because, in intensively farmed species-poor landscapes, dispersal limitation may constrain positive effects of local management on species richness (van Nouhuys, 2005; Rand et al., 2006). Biocontrol management that depends on rich enemy communities or with conservation objectives should focus on agroecosystems near natural, species-rich areas with source populations and high noncrop–crop spillover (Bianchi et al., 2006), while local management, aimed at enhancing biological control of common generalist enemies, can be implemented in the wider countryside. Generalist enemies may even profit from simplified landscapes with their highly productive agroecosystems enhancing crop–noncrop spillover (Rand and Tscharntke, 2007). Generalist predators with high dispersal abilities, using a wide range of managed and natural habitats covering broad spatial scales, are suited to the highly disturbed, human-dominated landscapes and are essential for sustainability in biocontrol following local disturbances (Tscharntke et al., 2005a,b).

A caveat for reliable recommendations of local and landscape planning for biological control is the increasing evidence that multitrophic level interactions are important for biological control, but are not yet understood at a landscape scale. For example, entomopathogenic fungi may interfere with arthropod predation (Roy et al., 2006) and may also change dispersal behavior of host insects, thereby affecting the spatial scale experienced. Belowground processes affect aboveground biocontrol via plant-mediated effects (Wardle and van der Putten, 2002; Poveda et al., 2005), but scale-dependence of such interactions needs to be explored.

In intensively farmed, structurally poor agricultural landscapes, creation of perennial boundary vegetation and other forms of local management (Corbett and Rosenheim, 1996; Thies and Tscharntke, 1999) or even a generally increased landscape complexity may enhance biodiversity and ensure naturally occurring biological control, as suggested by the insurance hypothesis (Bengtsson et al., 2003). In contrast, local management in structurally complex landscapes may have little effect on local species richness or ecosystem processes but may still enhance enemy population densities resulting in biological control benefits (Tscharntke et al., 2005b). Hence, spatially differentiated land-use implementation and sound scientific knowledge of the ecology of the target species groups should be the basis of successful management decisions at local and landscape levels, because responses differ between species groups and often even between species. Poor knowledge of the relative role of the composition and configuration of agricultural landscapes for maintaining a diversity of biocontrol agents contrasts with its importance for sustainable crop production.

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