

The landscape context of trophic interactions: insect spillover across the crop–noncrop interface

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Landscape structure influences local diversity and ecosystem processes, including cross-habitat fluxes of organisms coupling the dynamics of different habitats. The flow of organisms across system boundaries is known to occur between different natural habitats as well as across the crop–noncrop interface. Several studies show how field boundaries can enhance predator populations invading arable crops and controlling pest populations. However, generalist arthropods may also spill over from land-use systems to natural areas (mainly grassland) modifying interactions therein. A view of land-use systems as sources and natural habitats as sinks is consistent with the idea that the direction of the organisms' fluxes is from high to low productivity systems, while noncrop habitats are important sources for recolonization of arable fields after they are cleared for harvest. From the perspective of landscape management, enhancement of population exchanges between crop and noncrop areas may include beneficial as well as unwelcome interactions.

Introduction

The importance of space for population dynamics and community ecology has been increasingly recognized during the past decades (Kareiva 1990, Ricklefs & Schluter 1993, May 1994, Kareiva & Wennegren 1995, With & Crist 1995, Polis *et al.* 1997, 2004, Holt 2002, Ries *et al.* 2004). Empirical evidence is growing that the distribution and abundance of populations and their biotic interactions often depend on processes occurring at spatial scales larger than the local habitat patch. Processes determining patterns of diversity and interactions occur not only on a local (site) scale, but also at the land-

scape scale, “the gray 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 systematists” (Holt 1993, *see* Bestelmeyer *et al.* 2003).

Concepts in spatial ecology are also important for applied reasons, because agroecosystems such as arable fields are characterized by organisms moving between crop and noncrop habitat. The ephemeral nature of arable fields, which are cleared during harvest, essentially resulting in “defaunated islands”, make colonization from the outside a central driver of community structure and beneficial interactions such as biological

control (Tscharrntke & Kruess 1999). In contrast, the high productivity of arable fields within the season greatly enhances density of many populations and may lead to an export of organisms to the surrounding landscape. Management of diversity and ecosystem services in agriculture should take such spillover effects into account in the context of a broader landscape perspective (Landis *et al.* 2000, Schmidt & Tscharrntke 2005b). Only recently, the importance of trophic cascades (predator-induced decreases in herbivore densities and plant damage) and top-down control has been acknowledged to be important in terrestrial (not only aquatic) ecosystems, and in both agricultural and natural systems (recent reviews by Schmitz *et al.* 2000, Halaj & Wise 2001, Scheu 2001, Walker & Jones 2001, *see* Terborgh *et al.* 2001). This goes along with a renewed interest in the improvement of farming practices and conservation biological control (Barbosa 2003, Snyder *et al.* 2005).

Cross-habitat foraging by consumers, herbivores and predators, may couple the dynamics of distinct habitats or landscape elements. An important concept emerging from this area of research is that resources present within one habitat type or system may subsidize shared consumers such that they have greater impacts on resources within a second system (i.e. can deplete resources to a greater degree) than would be expected based on *in situ* dynamics alone (Polis *et al.* 1997). This produces an interaction parallel to apparent competition (i.e. indirect interactions between two species via a shared enemy or a third, mutualistic or competitive, species at the same trophic level; Holt 1984). Such cross-boundary subsidies have been found to be important in linking the dynamics of a variety of natural systems (Polis *et al.* 1997, 2004). For example, insects supported by marine or aquatically derived primary production can subsidize predators, such as spiders and lizards, thereby modifying the impacts of these predators on terrestrially based prey communities (Polis & Hurd 1995, Sabo & Power 2002).

Cross-system fluxes of organisms can similarly occur across natural-anthropogenic habitat interfaces, and are an important mechanism by which habitat fragmentation may influence ecological dynamics within remaining habitat

remnants (Janzen 1983, Andren & Angelstam 1988, Cantrell *et al.* 2001, Holt & Hochberg 2001). Some of the best examples of the potential importance of cross-habitat foraging by generalist natural enemies come from studies of bird populations in fragmented forests. For example, Angelstam (1986) found that predation on experimental nests was positively related to the abundance of corvid birds, which was in turn positively related to the proportion of agricultural land, human population density and the degree of forest fragmentation across a regional gradient. Brood parasitism by cowbirds, also known to benefit from agricultural habitat, has similarly been found to increase near forest fragment edges in a number of studies (Paton 1994, Ries & Sisk 2004).

There has been much interest in the movement of insects between natural and agricultural systems, although the focus has generally been on implications of such movement for the functioning of agroecosystems (Ekbom *et al.* 2000). For example, the elimination of wild or weedy plants, which can serve as secondary host sources or “reservoirs” of insect pests colonizing crop fields, is considered an important component of cultural pest control (Herzog & Funderburk 1986). At the same time, natural habitats are recognized to provide important resources (pollen, nectar, alternative hosts, over-wintering sites) for insect natural enemies attacking crop pests (Landis *et al.* 2000). Studies have increasingly taken a landscape scale approach to examining such dynamics, demonstrating that factors such as habitat diversity, or the proportion of natural habitat within agricultural landscape mosaics, can greatly increase the abundance, diversity and impact of natural enemies within agroecosystems. In stark contrast to the growing number of spatial studies demonstrating the importance of natural or semi-natural landscape elements for insects within agroecosystems, however, very little work has examined the potential impact of such shared consumers on the “alternative” resources occurring within the remaining natural habitats themselves.

In the following sections, we will focus on a major landscape effect, the spillover of organisms from one habitat to another and discuss its importance for crop–noncrop interchanges in

agricultural landscapes. The flow of organisms across system boundaries, or between different habitat types, is increasingly recognized to be an important factor influencing *in situ* food web dynamics within ecological communities (Polis *et al.* 1997, 2004). First, we assess to what extent current theoretical approaches address effects of cross-habitat fluxes of organisms. Second, we review the importance of natural habitats acting as sources of natural enemies that colonize crops and control pest populations. Third, we provide an overview of spillover of natural enemies and herbivores from crops to natural habitats. Fourth, we show that enhancement of biotic interactions due to crop–noncrop spillover can be beneficial or conflicting, and we end the review with concluding remarks.

Cross-habitat fluxes: limitations of metapopulation theory

Island biogeography (MacArthur & Wilson 1967) and metapopulation theory (Hanski 1999) are classical and important concepts in spatial ecology, but reduce landscapes to habitat patches within a matrix of nonhabitat (cf. van Nouhuys 2005, Hanski & Meyke 2005). Terrestrial habitats, however, are not as sharply isolated as marine islands by the sea, because the composition of the landscape surrounding terrestrial habitat islands may differ in many ways (Tscharntke & Brandl 2004). The simplistic view of patch–non patch landscapes is advantageous for the development of predictive models, but is of limited value for understanding the complexity of between-habitat interactions in many landscapes. Limitations of island biogeography include the focus on saturated communities stabilized by a colonization–extinction equilibrium. There is, however, increasing evidence of largely unsaturated and non-equilibrium communities (Gaston & Spicer 2004). Limitations of metapopulation theory become evident when the landscape matrix inhibits or facilitates dispersal (Ricketts 2001, Cronin 2003), as dispersal limitation is often related to landscape composition and functional habitat connectivity changes with landscape composition. The composition of matrix habitat may also influence the quality

of host-plant patches (Haynes & Cronin 2004). Metapopulation theory also ignores non-habitat patches influencing adjacent patch occupancy and the use of a continuum from low to high quality patches or even different patch types (Baguette 2004, Shreeve *et al.* 2004 vs. Hanski 2004, Tscharntke & Brandl 2004). In addition, edge effects as well as spillover effects are important processes that should be addressed (With & Crist 1995, Ries & Sisk 2004, *see* the contribution of Harrison *et al.* 2005). The fact that regional species pools determine the diversity of local communities and their interactions also calls for adopting a landscape perspective (Holt & Gaston 2002). Further, resource use of many if not most species is not restricted to a single habitat, but allows utilization of different parts of the landscape (Dunning *et al.* 1992, Kareiva & Wennergren 1995). Habitats of such multi-habitat users are often spatially separated, for example bees need flowers and nesting sites, parasitoids need nectar for adult feeding and hosts for larval development, and many crop pests hibernate in near-natural habitats (*see* Dunning *et al.* 1992). Populations experience the landscape at different spatial scales contingent on body size, dispersal behaviour, functional group and trophic level (Kareiva 1990, van Nouhuys 2005). Hence, interacting populations are influenced by their species-specific functional scales, which may ultimately alter the nature or strength of biotic interactions (Tscharntke & Brandl 2004).

Invasion of predators in crop fields from adjacent natural habitats

Natural pest control is an important ecosystem function that often depends on colonization of arable crops by natural enemies. Natural enemies have been reported to invade arable fields, and reduce pest densities, thereby reducing damage levels and mitigating yield loss (Cardinale *et al.* 2003, Östman *et al.* 2003). Therefore, an abundant complex of natural enemies in crops may provide sustainable crop protection, reducing the need to use chemical pesticides. However, crops are difficult environments for many natural enemies because they are transient habitats

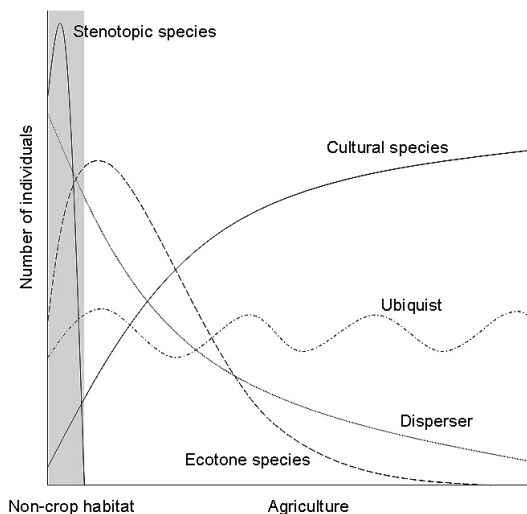


Fig. 1. Five types of distribution patterns of insects across the crop–noncrop interface. The non-crop habitat is indicated by the grey area (after Duelli & Obrist 2003). Stenotopic species are restricted to non-crop habitats, cultural species have a preference for crops, dispersers colonize crops from non-crop habitats, ecotone species are typically found at the interface of crop and non-crop habitats and ubiquitous species have no preference for crop or non-crop habitats.

subject to frequent and intensive disturbances (Marino & Landis 2000). For instance, pesticide applications and cultivation practices may cause strong reductions in natural enemy populations (Longley *et al.* 1997, Thomas & Jepson 1997). As a consequence, arable fields depend on colonization of natural enemies from other habitats early in the season or after disturbances (Wissinger 1997). Non-crop habitats such as woodlots, hedgerows, hedges, field margins and fallows are relatively undisturbed and permanent habitats that provide essential resources for natural enemies. Many natural enemies use natural habitats for finding alternative prey, plant food sources, a favourable microclimate, refuge and hibernation sites (Landis *et al.* 2000, Gurr *et al.* 2003). As a consequence, non-crop habitats may act as sources of natural enemies that may invade crops and control pest populations.

The spatial distribution of natural enemies in crop habitats has important implications for their potential as pest control agents. Duelli and Obrist (2003) distinguish five types of distribution patterns of insects in agricultural landscapes

(Fig. 1). “Stenotopic species” are specialists for non-crop habitats and are hardly found in crops. Ground beetles of the genus *Amara* (Carabidae) are representative of this group as they only occur in hedgerows, and do not penetrate crops (Thomas *et al.* 2001). In contrast, “cultural species” have a preference for crops and occur only sparsely in non-crop habitats. Examples of cultural species are ground beetles of the genus *Pterostichus* that occur in crops during the growing season and may hibernate in field margins or in fields with winter crops (Duelli *et al.* 1990, Booij *et al.* 1995). “Dispersers” and “ecotone species” colonize crops from non-crop habitats but densities remain higher near the field edge than in the field interior. This distribution pattern may be observed in species groups that frequently commute between crop and non-crop habitats, such as lacewings *Chrysopa* spp. (Freeman Long *et al.* 1998). Finally, “ubiquists” occur both in crop and non-crop habitats without a specific preference for one habitat type or the other. Such a distribution pattern may result from non-directed passive dispersal by wind resulting in an even distribution of colonizing insects over large areas, as observed in ballooning spider species (Halley *et al.* 1996).

Besides the spatial aspects of colonization, the timing of field colonization may influence natural pest control as well. Generalist predators often invade crops early in the season when pest densities are still low (Settle *et al.* 1996, Petersen 1999), whereas specialist natural enemies typically arrive later in the season. Early in the season, when pest populations build up, removal of limited numbers of pests by natural enemies may prevent serious outbreaks later in the season. Once pest densities are high, numerical responses of predators are often not strong enough for pest suppression, so early colonization of crop fields by natural enemies is likely to boost natural pest control.

Groups of natural enemies differ with respect to their spatial and temporal colonization dynamics. Parasitoids are natural enemies that may control pest populations in crops typically in June, July and August (in central Europe), when pest populations are well established (Costamagna *et al.* 2004, Thies *et al.* 2005). Parasitoids often exhibit directed flight over relatively short

distances (Corbett & Rosenheim 1996b, Bellamy & Byrne 2001) and depend on non-crop habitats for floral nectar sources and a favourable microclimate, and on crops for hosts (Dyer & Landis 1996, Siekmann *et al.* 2001). As a consequence, parasitism levels generally decrease at further distance from field edges, reflecting distribution patterns of dispersers and ecotone species (Fig. 1). This pattern is reflected by decreasing parasitism levels at further distance from field edges. Depending on the parasitoid species, the distance of the enhanced parasitism effect may be in the order of tens (Baggen & Gurr 1998, Thies & Tschardtke 1999, Tylianakis *et al.* 2004) to hundreds of meters (Landis & Haas 1992, Freeman Long *et al.* 1998). Besides the directed flight over short distances, some parasitoid species may also disperse over several kilometres from overwintering habitats to summer habitats (Doutt & Nakata 1973, Corbett & Rosenheim 1996a, Bianchi *et al.* 2005).

Adult hoverflies (Syrphidae) are good fliers that show directed search for flowers and aphid colonies to deposit eggs (Cowgill *et al.* 1993, Scholz & Poehling 2000). In western Europe, carnivorous syrphid larvae emerge in crops around May–June (Chambers & Adams 1986, Krause & Poehling 1996). Adult syrphids aggregate in non-crop habitats that provide plant food sources leading to the accumulation of syrphids over areas well exceeding 200 m (Hickman & Wratten 1996, Freeman Long *et al.* 1998). In Dutch agricultural landscapes, D. Kleijn & F. Langevelde (unpubl. data) demonstrated a significant positive relationship between the abundance of syrphids and the proportion of non-crop habitat in a 1000-m radius. As a consequence, pest control by carnivorous syrphid larvae is influenced by the landscape scale, while effects of plant food sources on pest control are not likely to be observed at the field scale (Hickman & Wratten 1996).

Carabid beetles, staphylinids and many spiders are ground-dwelling predators that hibernate in non-crop habitats and invade arable fields in early spring. Colonization may take place as early as March in western Europe (Coombes & Sotherton 1986, Petersen 1999). Initially, the distribution pattern of ground-dwelling predators reflects that of dispersers (Coombes & Sotherton

1986, Thomas *et al.* 1991, Dennis & Fry 1992, Booij *et al.* 1995, Collins *et al.* 2002) with predators penetrating crops up to several hundreds of meters (Coombes & Sotherton 1986, Booij *et al.* 1995). Later in the season, the distribution pattern may change to that of cultural species, as reproduction may take place in the field (Duelli *et al.* 1990, Thomas *et al.* 1991, Collins *et al.* 2002).

Ballooning spiders, such as Linyphiidae, show non-directed movement over large distances using air currents (Bishop & Riechert 1990). Ballooning activity depends strongly on weather conditions, but may start as early as May (Topping & Sunderland 1998, Schmidt & Tschardtke 2005b). Emigrating spiders are distributed like a blanket over large areas in crop and non-crop habitats, reflecting the ubiquitous distribution pattern (Fig. 1). Non-crop habitats, which allow the long-term build-up of populations, function as sources of spiders (Halley *et al.* 1996, Schmidt & Tschardtke 2005a, 2005b). This is illustrated by a study of Schmidt and Tschardtke (2005b) who demonstrated a positive correlation between the density of webs in crop fields and the proportion of non-crop habitat up to 3000 m around the study plots.

In conclusion, non-crop habitats often act as sources of natural enemies. As a substantial part of the natural enemy complex is concentrated in the crop area near non-crop habitats (colonizers, ecotone species and cultural species at the start of field colonization), pest control may be enhanced in these areas (Bianchi & van der Werf 2003). Therefore, landscapes with many and extended interfaces between natural areas and arable fields may be subject to reduced pest pressure and may be less dependent on the use of chemical pesticides (Ohnesorge & Schier 1989, references cited in Schulze & Gerstberger 1993).

Spillover effects of predators and herbivores from crop fields into adjacent habitats

Generalist predators may also spill over from crop habitats to natural habitats. This may be expected in situations where generalist insect natural enemies exploit prey resources in crop-

ping systems as well as in adjacent natural habitats. Results of a study of aphidophagous coccinellid beetles, carried out in twelve replicate landscapes in the mixed grass prairie region of the central United States, support this idea (T. A. Rand & S. M. Louda unpubl. data). Coccinellid densities were almost five times higher in natural grassland sites that were embedded within crop-dominated habitats (>60% crop cover, mostly maize and soybean) as compared with those in sites surrounded by predominantly natural habitats (>90% mixed grass prairie) across the three years of the study. Beetle densities were also consistently higher (by a factor of 1.5 to 4 within crops than in adjacent grassland habitats throughout the summer (June–August), suggesting that cropping systems are potentially high-density sources of beetles. Finally, predator exclusion experiments carried out in four landscapes demonstrated that predators can greatly suppress the densities of a native thistle feeding aphid in natural grasslands, and predation pressure was strongly positively related to coccinellid densities. This study suggests that surrounding agricultural habitats can influence insect dynamics within remnant natural areas and, more specifically, that the abundance and potential impact of generalist predators may actually increase in natural areas occurring within landscapes moderately fragmented by agricultural land uses.

Additional anecdotal evidence of the potential importance of cropping systems in boosting coccinellid populations comes from the UK in 1976, when amazing migrations of ladybirds worried people all over the country. This spectacular ladybird plague was most likely prompted by high aphid densities in crops and favourable climatic conditions in 1975 and 1976 (Majerus & Kearns 1989). The abundance of spiders has similarly been found to increase at edges of experimental grassland plots (T. Jackson *et al.* unpublished data as cited in Debinski & Holt 2000). This effect was attributed to the ability of spiders to benefit from the aerial drift of prey species originating from the surrounding landscape, which consisted mainly of productive mown turf.

Crop–noncrop spillover effects are also known for herbivorous insects. In one of the few studies to explicitly examine spillover of herbiv-

orous insect pests from agricultural edges into natural habitats, McKone *et al.* (2001) examined the abundance of corn-rootworm beetles (*Diabrotica* spp.) in a tall grass prairie fragment in the central United States, in relationship to distance from surrounding maize fields. Substantial numbers of adult beetles, which are important pests of maize early in the summer when the larvae feed on roots, were found invading prairie habitats in late summer, after suitable resources within fields (maize reproductive tissues) began to desiccate. Beetle abundance was strongly related to the distance from a maize field edge. For example, densities of *Diabrotica barberi* were 18 times higher adjacent to maize as compared with those 170 m away. The abundance of beetles and floral damage on potted native sunflowers, *Helianthus annuus*, declined with distance from maize fields. Since pollen feeding by *Diabrotica barberi* was found to reduce seed set of *Helianthus annuus*, the authors suggest that this agricultural pest may interfere with the reproduction of native sunflowers and other late flowering composites (McKone *et al.* 2001). This study provides a clear example of the potential importance of cross-habitat movement of herbivores in modifying the intensity of ecological interactions (herbivory) at edges of remaining natural habitat.

Evidence for herbivore spillover from crop to natural areas comes also from studies on abundance–area relationships. In a study of butterfly communities on calcareous grassland fragments in Germany, which were embedded in an agricultural landscape, Steffan-Dewenter and Tscharrntke (2000) found that densities of generalist, polyphagous and oligophagous butterfly species increased with decreasing fragment area, presumably due to the accumulation of individuals from the surrounding landscape (*see also* Summerville & Crist 2004).

These examples suggest that the spillover of generalist arthropods from anthropogenically modified habitats of the surrounding landscape can increase their abundances either within habitat edges, or in smaller fragments, and in some cases may modify species interactions within remaining natural areas. Although little empirical work has explicitly addressed spillover effects of insects from agricultural to natural systems, it may be a common phenomenon, as many her-

bivorous agricultural pest and beneficial natural enemies are polyphagous and share both habitat types (Symondson *et al.* 2002). For example, the tarnished plant bug, *Lygus rugulipennis*, a major pest in many cropping systems has been recorded on 437 plants in 57 families (Holopainen & Varis 1991). A number of broadly distributed pest aphid species including *Myzus persicae*, which attacks a wide variety of crops including oilseed rape, sugar beet and tobacco, *Acyrtosiphon pisum*, a common pest of forage crops, such as red clover and lucerne, and *Sitobion avenae*, which commonly attacks cereals, have all been documented feeding on native plants in the U.K. (Müller *et al.* 1999). Oilseed rape has been found to host a number of herbivore species which are also found on wild *Brassica* species in central Germany (S. Tommes *et al.* unpubl. data). Similarly, many predators considered to be important within agroecosystems, such as carabid beetles and spiders, are generalists that use resources provided by natural habitats (Landis *et al.* 2000, Symondson *et al.* 2002). Coccinellid beetles, although often considered “aphid specialists”, actually attack multiple prey items, such as eggs and larvae of many insect groups, and feed on pollen (Hodek & Honek 1996). *Coccinella septempunctata*, a widely distributed and prevalent predator in many agroecosystems, has been found to feed on the eggs of native lycaenid butterflies, as well as larvae of other native coccinellid species in the United States (Horn 1991, Obrycki *et al.* 2000).

Even parasitoids are seldom strictly monophagous (Shaw 1994), and many biological control parasitoids also attack native species. For example, sixteen percent of 313 parasitoid species introduced to control holometabolous insect pests in North America have been documented from native hosts (Hawkins & Marino 1997), so many of these species seemingly dispersed from crop to noncrop habitats. More specifically, Barratt *et al.* (1997) found that the braconid parasitoid, *Microctonus aethiopoides*, introduced in New Zealand to control pest weevils in lucerne, also attacks a number of non-target indigenous weevil species in pastures and grazed natural grasslands. Parasitism rates on non-target weevils were particularly high at a grassland site located within a major lucerne growing region.

Here we provided just a few of the numerous examples in which agricultural and natural habitats share important consumers that have the potential to link their dynamics through spillover effects.

Although empirical examples are rare, some general principles may focus expectations of when and where spillover effects are likely to be important. Modelling and empirical work suggests that the direction of subsidized consumer effects is generally from high productivity to low productivity systems (Polis *et al.* 1997). It is notable that the two studies illustrating the potential importance of insect spillover from agricultural areas were carried out in the central United States, where cropping systems are highly productive, fertilized and irrigated monocultures juxtaposed with relatively arid natural grassland systems. Spillover effects may be expected to be less important in regions where the productivity differences between natural and cropping systems are less extreme, e.g. in many parts of central Europe. In addition, the temporal dynamics of resource availability is likely to influence spillover effects. For example, models suggest that if consumers and predators show a strong numerical response to temporal pulses in resource availability, they may exhibit unusually strong top-down effects on alternative prey species, which are available as the pulsed resource declines (Sears *et al.* 2004). Many cropping systems are ephemeral, providing ample and high quality resources during only a part of the season. Thus, stronger top-down impacts on alternative prey species may occur as resources within cropping systems are depleted or become unavailable, which is generally later in the growing season. Such temporal dynamics were likely an important factor driving the spillover of corn-rootworm beetles into tall grass prairie fragments in the example described previously. Similarly, disturbances, such as mowing or harvesting, may force surviving insects to seek refuges in natural or semi-natural habitats. For example, generalist predators (spiders, carabid and staphylinid beetles) left arable fields in response to a variety of crop management practices, which may result in the aggregation of predators in natural habitats (Thorbeck & Bilde 2004). Similar concentration or “crowding” effects have been

observed for insects in short-term experimental grassland fragmentation experiments (Collinge & Forman 1998), and may alter species interactions in remaining fragments (Saunders *et al.* 1991). These kinds of concentration effects may potentially increase herbivore and/or predator abundance in natural habitat fragments after disturbances in cropping systems.

Contrasting effects of the crop–noncrop interface

This review shows that agroecosystems may function as a source or sink for arthropods with corresponding spillover from anthropogenic to natural areas or vice versa. Hence, management of habitat allocation to promote ecosystem services in agricultural landscapes may be an ambiguous task. In addition to the direction of population flow, the enhancement of biotic interactions may be beneficial or conflicting. In general, landscape or local management aiming at enhancing biodiversity in agroecosystems may favour organisms of different functional groups and their interactions. Mutualistic interactions, such as plant–pollinator, plant–mycorrhiza or plant–parasitoid, as well as antagonistic interactions, such as plant–herbivore or plant–pathogen, may profit from these changes (Thomas 1989, Didham *et al.* 1996), showing the potentially conflicting nature of enhanced biotic interactions. Winter wheat fields in complex landscapes profit from higher aphid parasitism, but also higher crop-field colonization by the (host-alternating) cereal aphids resulting in aphid pest densities similar to those in simple landscapes (Thies *et al.* 2005). This is in contrast to the landscape-wide control of rape pollen beetles. Structurally complex landscapes cause higher parasitism of rape pollen beetles and, thereby, reduce the damage of this economically important rape pest (Thies & Tscharrntke 1999). The enhanced parasitism is due to old and grassy field margin strips, offering hibernation sites for these effective biocontrol agents. However, these grassy field boundaries also enhance slug populations that can cause great damage to rape seedlings (T. Tscharrntke pers. obs.).

Examples of such cross-system spillover span a spectrum from crop-dominated landscapes to

landscapes dominated by natural ecosystems. For example, complex landscapes cause more problems in crop fields with notorious weeds such as the thistle *Cirsium arvense*, due to fallow areas enhancing landscape-wide density of this weed invading arable crops (A. Kruess & T. Tscharrntke unpubl. data), in spite of more thistle antagonists (Kruess 2003). The large species pool in complex landscapes, however, also allows higher local diversity of non-crop plants in cereal fields (Roschewitz *et al.* 2005). Similarly, complex landscapes with a high diversity and mosaic of habitat types sustain higher bee diversity and higher pollination, but are also subject to increased (predispersal) seed predation, resulting in similar seed set as in simple landscapes (Steffan-Dewenter *et al.* 2001).

These examples showing mixed effects of the crop–noncrop interface illustrate that enhancement of biotic interactions through spillover effects need not meet management objectives *per se*. In many cases, the resulting interactions are of contradicting nature, making general recommendations for landscape management very difficult due to case-specific differences.

Conclusions

We conclude that the spillover of agriculturally subsidized insects has the potential to greatly influence plant–herbivore and herbivore–natural enemy interactions within remaining fragments of natural or semi-natural habitat, in spite of the little empirical evidence available to date. This conclusion is based on the general ecological patterns emerging from the literature on subsidized consumer effects and the ubiquity of examples suggesting that crops and natural habitats often share important insect consumers. The high productivity of crops and corresponding high population density of arthropods would be expected to result in widespread emigrations into adjacent natural areas. Complementary resource use appears to be often important, as crop habitats offer high amounts of food, while their ephemeral nature make supplementary resource outside the crop necessary (hibernation sites, nesting facilities, etc.). As a consequence, cropping systems will be highly dependent on surrounding

natural habitat as an initial source of insect colonists. The relative importance of the direction of such spillover effects across the crop–noncrop interface should be influenced by the relative productivity and temporal resource availability of each system. General predictions and management recommendations are even more difficult, as noncrop habitat can be a source or sink of both beneficial or unwelcome species. In addition, the potential importance of landscape structure for the spread of fungal diseases (Holdenrieder *et al.* 2004), the transmission of virus infections via insect vectors (Power & Mitchell 2004), the consumption of Bt pollen by herbivores (Losey *et al.* 1999) and the decomposition of organic matter (Hedlund *et al.* 2004) is largely unknown.

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