REVIEWS AND SYNTHESES

Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats

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Abstract

The cross-edge spillover of subsidized predators from anthropogenic to natural habitats is an important process affecting wildlife, especially bird, populations in fragmented landscapes. However, the importance of the spillover of insect natural enemies from agricultural to natural habitats is unknown, despite the abundance of studies examining movement in the opposite direction. Here, we synthesize studies from various ecological sub-disciplines to suggest that spillover of agriculturally subsidized insect natural enemies may be an important process affecting prey populations in natural habitat fragments. This contention is based on (1) the ubiquity of agricultural–natural edges in human dominated landscapes; (2) the substantial literature illustrating that crop and natural habitats share important insect predators; and (3) the clear importance of the landscape matrix, specifically distance to ecological edges, in influencing predator impacts in agroecosystems. Further support emerges from theory on the importance of cross-boundary subsidies for within site consumer–resource dynamics. In particular, high productivity and temporally variable resource abundance in agricultural systems are predicted to result in strong spillover effects. More empirical work examining the prevalence and significance of such natural enemy spillover will be critical to a broader understanding of fragmentation impacts on insect predator–prey interactions.

Keywords

Agroecosystem, biological control, consumer, cross-boundary, cross-system, edge effects, fragmentation, herbivore, spatial subsidies, spillover predation.

Ecology Letters (2006) **9**: 603–614

INTRODUCTION

Habitat loss and fragmentation are major causes of biodiversity loss and native species endangerment (Wilcove *et al.* 1986, 1998; Saunders *et al.* 1991). Recent syntheses have emphasized the key role that edge effects can play in fragmentation dynamics (Murcia 1995; Laurance *et al.* 2002; Ries *et al.* 2004). Edge effects are likely to become increasingly important as habitat loss progresses, resulting in ever smaller natural habitat fragments with a concomitant increase in their edge-to-interior ratios. Thus, understanding the influence of edges on ecological dynamics is fundamental to a broader understanding of the impacts of habitat loss and fragmentation on natural populations and communities (Fagan *et al.* 1999; Ries *et al.* 2004).

Changes in ecological characteristics in relation to proximity to 'edges', which we define simply as the boundary delineating two distinct habitat or vegetation types, have long been studied in wildlife conservation (Fagan *et al.* 1999; Ries *et al.* 2004). The traditional focus has been on pattern, for example documenting changes in abiotic environmental variables, or shifts in the diversity and abundance of organisms, in relation to distance from habitat edges. However, Fagan *et al.* (1999) noted a more recent shift in interest towards understanding the mechanisms via which edges alter ecological processes. They suggest that

cross-boundary subsidies, in particular the external acquisition of resources coupled with cross-edge dispersal of organisms, represent a potentially important class of such edge-mediated effects. This contention is supported by earlier work suggesting that cross-edge spillover of mobile antagonists, such as competitors and natural enemies, from surrounding matrix habitats can exert strong negative effects on resident species within remaining natural habitats (Janzen 1983, 1986; Suarez et al. 1998). Additional theoretical work further underscores, the important role that 'spillover-predation' or predator 'cross-edge incursions' may play in determining the persistence of within patch prey populations (Oksanen et al. 1992; Cantrell et al. 2001; Schneider 2001; Cantrell et al. 2002).

To date the literature on the importance of spillover processes in mediating natural enemy abundance and impacts near habitat edges has focused on vertebrate populations, with the vast majority of studies carried out on birds. Many empirical studies have documented increased avian nest predation or parasitism near habitat edges in fragmented landscapes (Paton 1994), although predator responses can vary depending on the species, scale and type of landscapes examined (Chalfoun et al. 2002). Elevated predation rates have in some cases been linked to increases in predator populations resulting from their use of agricultural habitats (Andrén et al. 1985; Andrén 1992; Huhta et al. 1996). Such studies provide strong empirical support for the idea that anthropogenic land-use systems may provide important subsidies to generalist predators, resulting in increased impacts on prey populations within adjacent habitats.

The effects of fragmentation and habitat edges on avian nest predation and brood parasitism have been the subject of no fewer than seven review papers over the last 10-plus years (Paton 1994; Andrén 1995; Hartley & Hunter 1998; Soderstrom 1999; Lahti 2001; Chalfoun et al. 2002). The most inclusive of these reviews included 55 studies on the topic (Lahti 2001). In contrast, in a search of biological databases (web of science and biological abstracts) and extraction of relevant references from a recent review (Ries et al. 2004), we found only one study that explicitly measured rates of insect natural enemy attack on native insects in relation to distance from anthropogenic edges. In this study, McGeoch & Gaston (2000) found that pupal, but not larval, parasitism of the holly leaf miner, *Phytomyza ilicis*, was higher at woodland fragment edges adjacent to roads and residential areas than in woodland interiors. They suggest that this may have been related to high levels of unexplained larval mortality at edges which resulted in low pupal numbers there, rendering it difficult to distinguish between potential underlying mechanisms. Several additional studies, discussed below, have quantified the abundance of arthropod predators in natural habitats near

agricultural edges vs. natural habitat interiors (e.g. Duelli et al. 1990; French et al. 2001; Martin & Major 2001; Baldissera et al. 2004; Rand & Louda 2006). However, none of these studies have explicitly examined the functional implications of such patterns.

Here, we draw on evidence from the agricultural literature to argue that spillover (i.e. the movement of subsidized natural enemies across agricultural-to-natural habitat edges) is likely to be an important process affecting insect herbivore populations, as is often observed for their well-studied vertebrate counterparts. We further suggest that the broader literature on cross-boundary subsidies (Polis et al. 1997, 2004) provides a useful theoretical framework to guide research on the influence of predator spillover on trophic dynamics in arthropod communities and beyond. Finally, we briefly enumerate the potential implications of predator spillover for the more general discussion of the effects of habitat fragmentation on insect food web dynamics, and call for more research on this potentially important yet markedly understudied topic.

SHARED PREDATORS AND THE POTENTIAL IMPORTANCE OF SPILLOVER ACROSS CROPLAND–NATURAL EDGES

Studies focused on cropping systems have demonstrated that insects are greatly influenced by landscape structure over a range of spatial scales (Tscharntke et al. 2005). For example, the abundance, diversity and/or potential impact of insect natural enemies have been shown to increase with increasing area or diversity of non-cultivated habitat in the landscapes surrounding crop fields. This has been demonstrated for both generalist predatory insects such as coccinellid beetles (Elliott et al. 1999, 2002a,b) as well as the more specialized parasitoids (reviewed in Cronin & Reeve 2005). Even natural-enemy 'edge effects', although rarely termed such, are often observed in cropping systems (Duelli et al. 1990; Dyer & Landis 1997; Thies & Tscharntke 1999; Tylianakis et al. 2004; Clough et al. 2005). Such increased natural enemy abundance, activity or impact near crop field edges, compared with field interiors, is often attributed to the proximity to important alternative resources. For example, natural or semi-natural habitats may provide over-wintering sites, alternative host species, or alternative energy sources that are critical to sustaining enemy populations (Landis et al. 2000; Tylianakis et al. 2004). Thus, in general, agroecosystem studies suggest that natural habitats can be important sources of natural enemies colonizing crop fields, and proximity to such habitats may result in increased control of agricultural pests (Landis et al. 2000).

Proximity to habitat edges is likely to be similarly important in driving patterns of predator abundance and impact within remaining natural habitats. Indeed, a number

of characteristics of agricultural systems may make them particularly prone to exporting predators to surrounding areas during at least some portion of the growing season. For example, temporal shifts in resource availability may result in shifts in the direction of predator dispersal through time. In addition, increases in predator abundance near edges, due to complementary resource use, would be expected to increase their impacts in adjacent natural habitats as well as cropping systems. Surprisingly, we were unable to find any published studies examining the importance of the spillover from the cropland 'matrix' in driving patterns of predator abundance and impact on native herbivores near natural fragment edges vs. interiors. However, a recent study by Rand & Louda (2006) suggests that such effects are likely to be important at landscape spatial scales. They found that the abundance of predatory coccinellid beetles was generally higher in cropland than in natural grassland habitats. In addition, coccinellids were three to six times more abundant at native grassland sites embedded within cropland-dominated landscapes compared with control sites in grassland-dominated landscapes, suggesting spillover effects. Similar patterns have been documented for herbivorous insects by McKone et al. (2001). They found that adult corn-rootworm beetles (*Diabrotica* spp.), which feed in corn fields as larvae, spill over in large numbers into adjacent tall-grass prairie causing increased damage to native plants growing near the prairie fragment edge. Despite the general paucity of empirical data examining insect spillover across cropland–natural interfaces, a number of observations combine to suggest this could be an important driver of predator impacts on native insect herbivore populations within natural habitat fragments.

First, habitat loss due to agricultural intensification is a primary cause of landscape change (Vitousek et al. 1997; Tilman et al. 2001), and in regions with modern agriculture, habitat loss at the landscape scale has often reached 80% or greater (Saunders et al. 1993). Tilman et al. (2001) predict that if past trends continue, 10^9 hectares of natural habitat would be converted to agriculture by 2050. Thus, agricultural systems make up an increasingly dominant component of modern landscapes, and cropland–natural interfaces represent a ubiquitous edge type within such landscapes. In highly fragmented ecoregions, such as the tall grass prairie of the central USA or parts of the wheat belt of western Australia, < 10% of the native vegetation remains. In such regions, most remnant natural habitat is likely to occur in relative proximity to agricultural edges and is thus potentially vulnerable to spillover effects.

Second, a primary requirement for the occurrence and importance of predator spillover across cropland–natural habitat edges is that the predators are habitat generalists that exploit prey resources within both habitat types (contrast Fig. 1a with Fig. 1b). This will not always be the case, as some predator groups, or species, show strong preferences for natural systems (Martin & Major 2001; Baldissera et al. 2004), while others remain largely confined to cropping systems (Duelli et al. 1990; Orr et al. 2000). However, on the whole, cropping systems support a diverse and abundant group of polyphagous predators and parasitoids, many of which utilize resources in adjacent semi-natural (e.g. fallows, field margins and hedgerows) or natural habitats (Landis et al. 2000). In fact, a majority of the predator groups known to be important in the suppression of crop pests (e.g. carabid, staphylinid and coccinellid beetles, spiders, hover flies and lace wings) are also known to use both woodland and herbaceous habitats extensively and presumably feed on alternative hosts within these natural systems (Symondson et al. 2002). Thus many natural enemies are likely to move extensively between cropland and natural habitats.

Further evidence for the use of native prey species even by insect parasitoids, which are generally considered to have narrower host ranges than the predator groups mentioned previously, comes from the literature on non-target effects of biological control. For example, Hawkins & Marino (1997) found that 16% of 313 parasitoids species introduced to control holometabolous insect pests in North America also attack native hosts. Even more striking, in a field based survey of a native forest in Hawaii, Henneman & Memmott (2001) found that 83% of parasitoids reared from native moth species in Hawaii were biological control agents, compared with only 3% native species. Similarly, in a more detailed case study, Barratt et al. (1997) found that the braconid parasitoid, *Microctonus aethiopoides*, introduced to control pest weevils in lucerne, also attacks a number of non-target indigenous weevils in pasture and grazed natural grasslands of New Zealand. Thus, even purportedly 'specialized' natural enemies, introduced specifically for the control of agricultural pests, can attack native species in natural habitats. In addition, modelling studies suggest that spillover effects can result in magnified impacts of biocontrol agents on non-target host populations even when target and non-targets occur within spatially distinct habitat types (Holt & Hochberg 2001), such as cropland and natural systems. Such spillover effects could theoretically result in increased vulnerability of native herbivore species to non-target attack near edges adjacent to cropland habitats which contain targeted hosts.

In general, we suggest that the spillover of agriculturally subsidized insects, both species specifically introduced for biological control as well as native species which simply benefit from prey resources in agricultural systems, has the potential to greatly increase predator impacts on native insect prey species in fragmented habitats. This contention is based on (1) the ubiquity of agricultural–natural edges in increasingly human dominated landscapes; (2) the substantial literature illustrating that crop and natural habitats can

share important insect consumers; and (3) the clear importance of the landscape matrix, specifically distance to ecological edges, in influencing predation pressure on pests in agroecosystems. Further support for this idea emerges from theory relating to the importance of cross-boundary subsidies for within site consumer–resource dynamics (e.g. Polis *et al.* 1997, 2004), which we discuss in the following section.

CROSS-BOUNDARY THEORY AND SPILLOVER EDGE EFFECTS IN AGRICULTURAL LANDSCAPE MOSAICS

Ries *et al.* (2004) suggest that progress in understanding the diverse ecological responses to habitat edges has been hampered by the lack of a unifying conceptual framework to guide research. They alleviate this problem with a conceptual model outlining the critical mechanisms and causal pathways potentially influencing organismal distribution and abundance patterns near habitat edges. This model highlights the central role of ecological flows (i.e. the movement of energy, materials and organisms across edges), and the potential influence of differences in quality of juxtaposed habitats, in generating different types of edge responses. The flow of materials and organisms has similarly been recognized to play a more general role in linking food web dynamics across a diversity of natural ecosystems over a range of spatial scales (Polis *et al.* 1997, 2004; Knight *et al.* 2005). However, the conceptual link to this important body of research is rarely made in the discussion of edge effects (but see Fagan *et al.* 1999; Cantrell *et al.* 2001). This may result from the fact that the latter has tended to focus on linkages across natural ecosystem boundaries, for example marine–terrestrial or aquatic–terrestrial interfaces (but see Power *et al.* 2004; Riley & Jefferies 2004), whereas the more recent literature on edge-effects has often focused on natural–anthropogenic interfaces. In any case, this work provides theory useful in making predictions regarding when and where spillover edge effects are likely to be important.

A basic insight to emerge from the literature on cross-system linkages is that resources present within one habitat type may subsidize shared consumers such that they have greater impacts on resources within a second habitat than would be expected based on *in situ* dynamics alone (Polis *et al.* 1997; Holt & Hochberg 2001). This interaction is similar to apparent competition (Holt 1984) and provides a theoretical basis for the expectation we described previously. That is, that shared generalist predator populations may be subsidized (i.e. maintained at high levels through numerical responses to resources in cropland systems) but disperse across edges, thereby increasing their abundance and impact on resident prey species in adjacent natural

habitats. Theoretical work suggests that resident prey species in recipient habitats will be particularly vulnerable to exclusion due to spillover predation when prey in these habitats exhibit low productivity, i.e. low intrinsic growth rates, relative to prey species in source habitats (Holt & Hochberg 2001). In addition, spillover predation is predicted to be particularly strong when (1) predator attack rates on prey in the recipient habitat are high; (2) predator movement rates are substantial; and (3) predator mortality rates in the recipient habitat are low (Holt & Hochberg 2001). High enemy dispersal rates have similarly been shown to increase the effectiveness of resource subsidies in promoting control of pest species in modelled agroecosystems (Kean *et al.* 2003).

Holt (1997) used predator–prey metapopulation models to examine the conditions under which spillover predation may be important at broader, landscape scales. He modelled landscapes composed of patches of two distinct habitat types, each containing a habitat specific prey species that shared a generalist predator. The model shows that when a predator is both a habitat and trophic generalist, alternative prey species specialized to different habitats may negatively interact via apparent competition. This can result in the regional exclusion of prey species, when predators are effective colonizers and can induce local prey extinctions. Prey species that are poor colonists, either due to poor individual dispersal abilities or low local population sizes, will be particularly vulnerable to exclusion via apparent competition at the landscape scale (Holt 1997). The extinction risk of a given prey species also increases when the level of predator control of the alternative prey species is not sufficient to risk local extinction, as this increases the fraction of the landscape that can harbour the predator (Holt & Hochberg 2001). Finally, a prey species will be more vulnerable to regional extinction when its habitat is scarce in the landscape, because this reduces the potential for recolonization following local extinction due to spillover predation (Holt 1997; Holt & Hochberg 2001).

Spatiotemporal variability in resource availability, and patterns of resource use, are additionally predicted to influence the direction and magnitude of spatial flows or spillover effects (Oksanen 1990; Holt & Hochberg 2001; Ries *et al.* 2004; Sears *et al.* 2004). In agricultural landscape mosaics, spillover edge effects could result from at least three distinct, yet potentially interrelated processes (Figs 1 and 2). First, assuming minimal effects of edges on animal movement, passive dispersal of shared predators across habitat boundaries would be expected to result in spillover of predators from high density source habitats into habitats with intrinsically lower enemy densities (Fig. 1b). Here, the direction and magnitude of spillover is likely to be highly dependent on the differences in primary productivity, and consequent differences in prey availability or quality, in

Figure 1 Simple conceptual models illustrating the effects of (a) habitat specialization, (b) differences in system productivity, and (c) complementary resource use on expected patterns of predator spillover across natural–agricultural habitat boundaries. y represents the base difference between the two habitats in productivity or carrying capacity. The depth of the edge influence x will be determined by dispersal capacity and/or foraging behaviour of predators. Both x and y are system specific, and y may take a negative value if predators in the crop habitat are subsidized by the natural habitat (e.g. Thies & Tscharntke 1999).
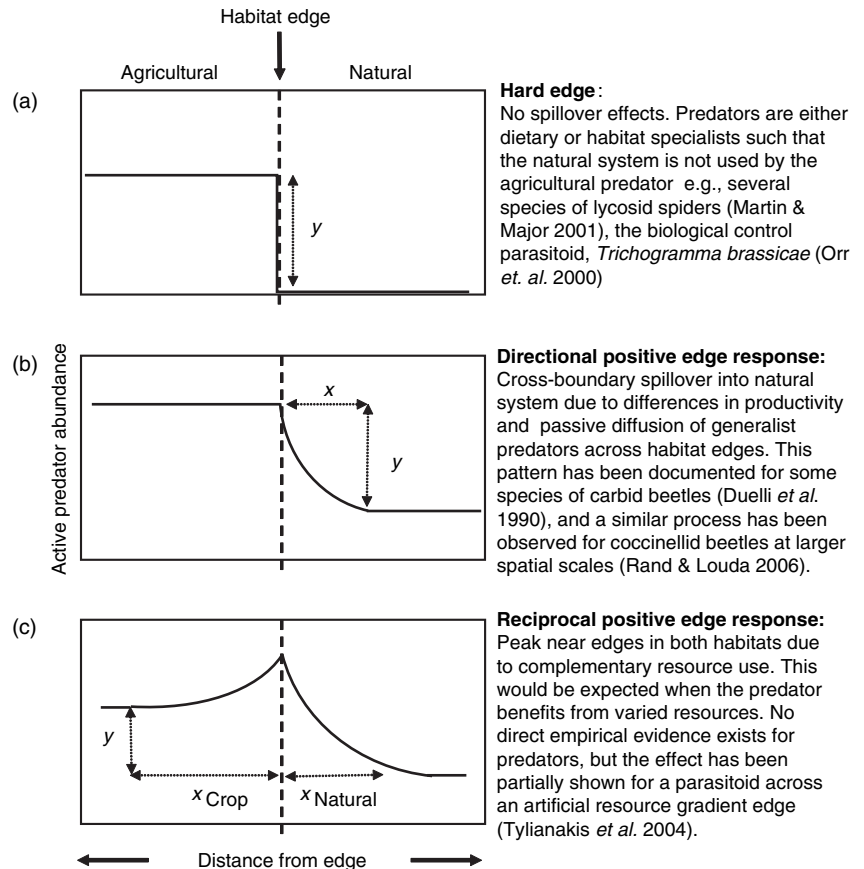
juxtaposed cropland and natural systems. Second, temporal declines in resource availability related to crop senescence or harvesting may result in the active emigration of predator populations, which have built up within cropping systems during the growing season, into adjacent natural systems (Fig. 2). Such declining resource quality in source habitats can result in transient spikes in predator density and impact on resident prey populations in remaining, recipient, habitats (Holt & Hochberg 2001). Finally, spillover effects may result from responses of predators to complementary resources in adjacent natural and cropland systems (Fig. 1c). In the following three subsections, we discuss each of these processes in more detail and review evidence for their potential importance for insects in agricultural landscape mosaics.

Spillover resulting from productivity differences in cultivated vs. natural systems

In general, both modelling and empirical work suggests that the direction of subsidized consumer effects is strongly asymmetric, affecting resources in low productivity systems more adversely than those in more productive habitats

(Oksanen 1990; Oksanen *et al.* 1992; Polis *et al.* 1997; Sears *et al.* 2004). For example, Oksanen (1990) found that in habitat complexes where a system of high primary productivity abounds, spillover predation can strongly impact populations of prey inhabiting the less productive habitat. This results, in part, because higher prey numbers in productive habitats lead to higher predator densities there. Increased predator densities in turn lead to higher rates of emigration to less productive habitats. Conversely, spillover predation is strongly diluted in habitat complexes dominated by a low productivity habitat (Oksanen 1990).

A logical prediction from this body of work is that spillover edge effects are most likely under conditions where a steep gradient in annual primary productivity is observed between two adjacent habitat types (i.e. large values of y; Fig. 1b), and when productive habitats make up a large proportion of a given landscape. As a whole, cultivated areas have higher estimated annual net primary productivity than most major natural terrestrial ecosystems, with a few notable exceptions such as tropical rain forests and savannas (Field *et al.* 1998). In many important agricultural regions, cropping systems are highly productive, fertilized and irrigated, monocultures juxtaposed with natural systems that exhibit
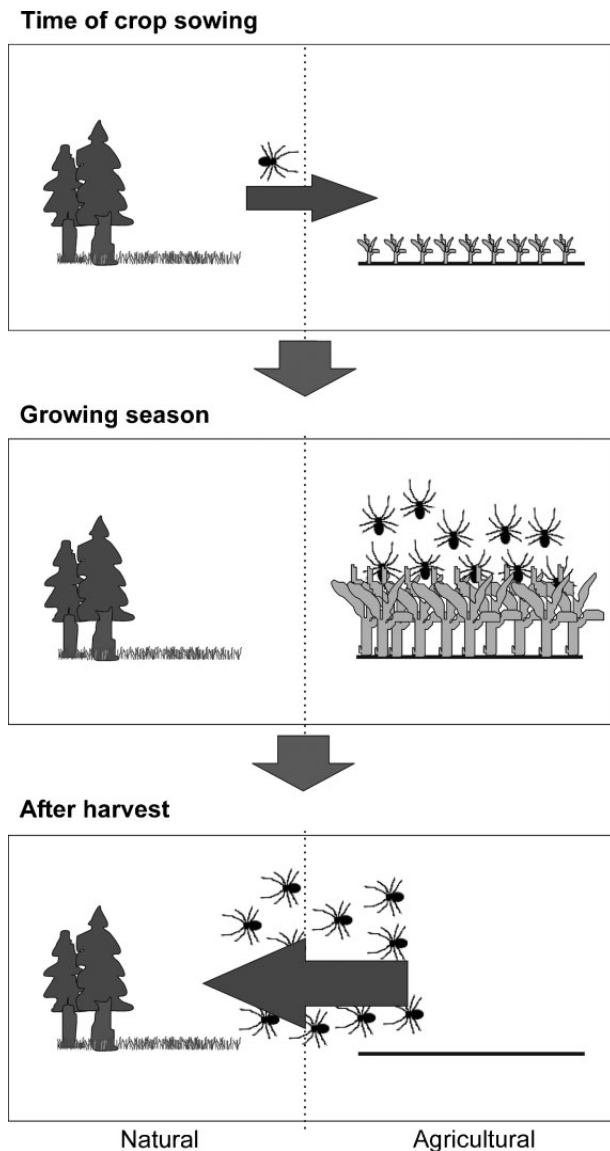
Time of crop sowing

Growing season

After harvest

Natural   Agricultural

Figure 2 Schematic diagram illustrating predator spillover resulting from temporal fluxes in resource availability in agricultural habitats. Predators initially colonize the cropland matrix from adjacent natural habitats. Predator populations then build up within the agricultural matrix during the growing season, due to feeding on crop herbivores. Finally, late season decline in resource quality within the agricultural matrix, due to crop senescence or harvesting, results in predator emigration and concentration within remaining natural habitats, potentially increasing predation pressure there.

lower productivity. For example, in a study conducted in the central USA, the annual production of organic matter in maize fields was found to exceed that of all associated natural ecosystems examined, and was an order of magnitude higher than in grassland prairie habitats (Ovington *et al.*

1963). Furthermore, habitat loss is often non-random (Seabloom *et al.* 2002), with relatively fertile lowland areas being more rapidly selected for conversion to agricultural land uses. This could magnify expected differences in productivity between cropping systems and remaining, inherently less productive, non-agricultural lands.

Productive cropping systems are prone to pest outbreaks, which in turn may result in a high quality resource base and the rapid build up of large predator populations. Thus, a basic prediction is that over the course of the growing season, higher overall productivity will result in prey population increases within cropping systems. This may subsidize shared predator populations, resulting in their spillover into adjacent natural habitats via passive diffusion (Fig. 1b). Such spillover processes would be expected to result in higher predator abundance and impacts near natural–agricultural habitat edges and in more fragmented landscapes. Moreover, such effects are likely to be especially important given the increasing dominance of agricultural habitats in many modern landscapes, which we discussed previously.

Spillover edge effects should be less important when less dramatic differences in system productivity, and subsequent prey availability, occur between natural and cropping systems. This may result from characteristics of the cropping systems themselves (e.g. inherently less productive crops, lack of irrigation and fertilization, crops supporting inherently low herbivore growth rates or densities, and insecticide application) or of adjacent natural ecosystems which vary greatly in annual net primary productivity (Field *et al.* 1998). Spillover of agriculturally subsidized predators may be generally more important for less productive natural systems, for example grasslands in arid temperate regions, compared with potentially more highly productive systems in moister tropical regions, such as rain forests. Under circumstances in which productivity of natural habitats exceeds that of cultivated lands, one might expect a reversal in the direction of subsidized consumer influences via passive processes.

Spillover resulting from temporally shifting resources

Temporal dynamics are also likely to play an important role in determining the magnitude and direction of cross-edge spillover. Models suggest that if consumers 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 (Holt & Barfield 2003; Sears *et al.* 2004). Spatial and temporal subsidies are often closely bound together, as transport through space is often seasonal (Sears *et al.* 2004). Holt & Hochberg (2001) have shown that in heterogeneous landscapes, a rapid decline in the suitability

of one habitat type can result in the emigration of mobile predators into an alternative, recipient, habitat. This can result in a transient spike in predator abundance in the recipient habitat, with numbers well above those which would be sustained by the *in situ* prey base. Such transient dynamics have the potential to greatly reduce prey numbers, and increase prey extinction risks, in recipient habitats (Holt & Hochberg 2001).

The relative availability of resources in agricultural and natural habitats will in most cases vary through time (Fig. 2). Many cropping systems are ephemeral, providing potentially high quality resources during only portions of the season over which insect parasitoid and predator populations are active (Wissinger 1998). For example, in temperate systems crops such as wheat mature and senesce relatively early in the growing season, while many native plants and insects are still active. Similarly, rice fields in some tropical systems are burned following harvest, such that fields are essentially barren for months afterwards. This can result in high temporal species turnover in mosaic landscapes containing crop and natural habitats (Tylianakis *et al.* 2005). Applying theoretical work to agricultural systems results in the basic prediction that top-down impacts on alternative prey species will be magnified as the once abundant resources within cropping systems become depleted, or unavailable, due to crop senescence or harvesting (Fig. 2). In this case, spillover should result from the active emigration of predators in response to declining habitat quality and their resulting concentration in adjacent natural systems rather than passive dispersal. Such temporal spillover processes may occur even in the absence of large productivity differences, since predators augmented by agriculturally derived resources are forced to emigrate upon crop senescence or harvesting. However, the magnitude of predator spillover and impact in the recipient habitat (natural systems in our example) should be greater if the source habitat has a larger intrinsic growth rate or carrying capacity (Holt & Hochberg 2001). In addition, predators with relatively short generation times, high reproductive rates and high vagility may more effectively respond numerically to high productivity and ephemerally available resources within cropping systems.

The potential importance of such temporal dynamics is supported by studies examining seasonal patterns in the abundance and movement of predators. For example, Duelli *et al.* (1990) estimated a seasonal production of 6000 adult coccinellid beetles from a single, 1 ha, maize field and documented a mass net emigration of beetles into adjacent habitats as within-crop aphid populations declined. Similarly, French *et al.* (2001) found that the number of carabid beetles captured in pitfall traps was generally higher at meadow edges than either meadow interiors or crop fields in the autumn, after wheat fields are harvested. In contrast, densities tended to be highest in wheat field interiors in the spring. This suggests that beetles may be leaving crop fields and concentrating in natural habitat edges as resources within cropping systems become unavailable. The high over-wintering densities of agriculturally important carabid and staphylinid beetles, which feed on crop herbivores during the growing season, in raised grass-sown strips referred to as 'beetle-banks' (MacLeod *et al.* 2004) are likely to be the result of similar processes. However, the manner in which these cross-system fluxes in predator abundance affect predation pressure on herbivores in adjacent natural systems remains to be investigated.

Disturbances such as mowing or harvesting may similarly force surviving insects to seek refuges in adjacent natural or semi-natural habitats. For example, generalist predators (spiders, carabid and staphylinid beetles) have been found to respond to a variety of crop management practices primarily by emigrating, which can result in the aggregation of predators in less disturbed habitats (Thorbek & Bilde 2004). Similar concentration or 'crowding' effects have been observed for insects in short-term experimental fragmentation experiments (Collinge & Forman 1998; Debinski & Holt 2000), and have been more generally postulated to alter species interactions within remaining natural habitat fragments (Saunders *et al.* 1991). Such concentration effects would generally be expected to increase consumer abundance and pressure at fragment edges, following declining resource availability or disturbances within surrounding cropping systems. However, overly frequent or severe disturbance regimes, that either prevent predators from building up within cropping systems or kill the majority prior to emigration, could in some cases obscure expected spillover effects.

Spillover resulting from complementary resource use

Spillover edge effects can also result when resources within natural and cropland habitats are complementary (Fig. 1c). This could result from either (or both) of two mechanisms. First, the aggregation of predators near edges, where they have access to both resources, would be expected to result in higher predator densities, and thus impact, in edge zones. Second, individual predators may exert increased per capita impacts, for example due to increased longevity or fecundity of individual predators when they are in close proximity to both resources. This may in turn increase population growth rates near edges, reinforcing the pattern of higher predator densities there. Once again, this process does not necessarily require large productivity differences between adjacent systems (i.e. higher predator abundance or impact at edges would be expected even without differences in y in Fig. 1c).

This mechanism is frequently studied with respect to the augmentation of biological control agents (Landis *et al.* 2000). A number of important predators in agricultural

systems exhibit life-history omnivory, resulting in their dependence on resources in both the agricultural and natural habitats. For example, female parasitoids and hover flies require herbivorous insects as hosts or prey for their larvae, but feeding on floral resources as adults increases their longevity and potential fecundity (Hickman *et al.* 1995). In such cases, proximity to external resource subsidies can increase the efficacy of biocontrol of crop pests (e.g. Tylianakis *et al.* 2004). Responses of predators to complementary resources may similarly increase predator abundance and impacts on native herbivores near natural habitat edges, but this has not been empirically examined. Examples of subsidies that individual predators could derive from the crop habitats include: floral nectar (Tylianakis *et al.* 2004), pollen (e.g. Hickman *et al.* 1995), alternative prey/hosts (e.g. parasitoids using alternative aphid hosts on sunflower crops; van Emden 1990) or aphid honeydew (e.g. Evans & England 1996).

Potential interacting or mitigating influences

Spillover processes might be influenced or mitigated by a number of additional factors, and we highlight two potentially key ones here. First, we have treated edges as simple boundaries between two habitat types, to which insects do not directly respond. However, edges can substantially influence animal behaviour, especially dispersal patterns (Strayer *et al.* 2003). Reflecting or absorbing edge conditions may modify predator densities at habitat edges from those expected from passive processes alone. For example, Haynes & Cronin (2003) found that planthoppers may be less likely to leave patches surrounded by a hostile matrix, which can result in their concentration at patch edges. Collinge & Palmer (2002) found that edge contrast strongly influences the movement of ground-dwelling beetles. Beetles were more likely to move into patches embedded within a low contrast matrix than a high contrast one. Finally, tree rows planted along field margins have been shown to impede the dispersal of flying insect predators (Wratten *et al.* 2003). Thus, spillover effects might be attenuated to some extent when edges reduce animal movement.

Second, a blending of the abiotic environmental characteristics of juxtaposed habitat types may create unique environments, resulting in altered vegetation structure and composition in edge zones (Laurance *et al.* 2002). Resulting shifts in herbivore communities may have bottom-up influences on the predator community and interactions. In such cases, shifts in predator communities near habitat edges will reflect their response to the altered resource base within the natural habitat itself, as well as any effects due to spillover of predators originating from external habitats such as agriculture. Furthermore, altered vegetation struc-

ture at edges may itself reduce edge permeability (Laurance *et al.* 2002).

IMPLICATIONS FOR INSECT FOOD WEB DYNAMICS IN FRAGMENTED LANDSCAPES

Studies examining the effects of habitat fragmentation on insect natural enemy–prey dynamics are often conceptually based in island biogeography or metapopulation theory. A long tradition of theoretical studies has examined the importance of spatial structure, or patchiness, for the stability of host–parasitoid dynamics (Briggs & Hoopes 2004). An increasing number have explicitly examined the potential effects of habitat loss on food web structure or predator–prey interactions (Kareiva & Wennergren 1995; Bascompte & Solé 1998; Holt *et al.* 1999; Swihart *et al.* 2001; Melian & Bascompte 2002). One prediction to emerge from theory is that specialist consumers should be more susceptible to fragmentation effects than their prey (Bascompte & Solé 1998; Holt *et al.* 1999). Therefore, prey may be released from control by specialist natural enemies with decreasing area or increasing isolation of remaining natural habitat fragments. There is considerable empirical support for this prediction at both population and community levels, particularly for insect parasitoids (see Cronin & Reeve 2005; van Nouhuys 2005). For example, studies of individual host parasitoid systems have found that parasitoids tend to be more extinction prone than their hosts (van Nouhuys & Tay 2001; Cronin 2004). Similarly, reduced area and/or increased isolation of habitat patches has been found to result in reduced parasitoid species richness and rates of parasitism (Kruess & Tscharntke 1994, 2000). Fragmentation may additionally disrupt predator foraging behaviour and the capacity of predators to control herbivorous prey populations (Kareiva 1987). Cumulatively, this body of patch-based theoretical and empirical work leads to the expectation that natural enemy pressure generally decreases with increasing habitat loss and fragmentation.

However, the extent to which natural enemies are disadvantaged by their higher trophic level position with increasing loss of natural habitats will depend on their ability to use the intervening modified matrix habitats. This, in turn, will depend on their level of trophic and habitat generalism (Holt *et al.* 1999; Tscharntke & Kruess 1999). In many cases, generalist species will not conform to predictions from 'island' or patch-based theoretical models. In fact, if the cross-edge spillover of generalist predators benefiting from resource subsidies in anthropogenic land-use systems turns out to be a generally important phenomenon, as we have argued is likely, then consumer pressure on herbivore populations might actually increase in fragmented habitats. We propose that the impacts of habitat

loss on insect natural-enemy prey dynamics will ultimately depend on the balance between declines in the abundance or diversity of specialist species, due to isolation and area effects, and the potential enhancement of generalist species due to spillover edge effects. The relative importance of these two processes in determining consumer pressure in fragmented landscapes remains a wide open area for future research. Assessing this balance will require shifting from a patch-based to a landscape-based approach, in which the suitability of the surrounding matrix for natural enemies is explicitly considered.

BEYOND INSECT COMMUNITIES

We have focused on the likely importance of spillover of insect predators and parasitoids, as they are an abundant and well studied group in agroecosystems. However, the same basic principles should apply more broadly to other groups of generalist natural enemies (primary as well as secondary consumers) that can benefit from resources within cropland habitats.

As noted previously, agricultural subsidies and spillover predation have been implicated as important processes limiting avian nesting success. Other examples might involve small mammals such as rodents, which are common generalist pests in agricultural habitats world-wide (Stenseth *et al.* 2003). Trapping studies have demonstrated temporal concentration effects similar to those observed for insects. For example, Jacob *et al.* (2004) documented an increase in rodent abundance in surrounding habitats after crop harvest, which was attributed to declining resource availability within crop fields. Such concentration effects could result in increased seed predation on native plants in the vicinity of crop fields. Additionally, strong numerical responses of small mammals to pulsed resources within natural habitats can result in cascading indirect effects through food webs. For example, mammal responses to seed masting events can subsidize generalist predators, such as owls, with potential indirect effects on alternative prey (Ostfeld & Keesing 2000). Pulsed resource availability within crop fields may result in similar processes.

Weeds and natural plant populations are known to be important reservoirs of crop pathogens. As with insects, the potential importance of the movement of pathogens in the opposite direction, i.e. from crops to surrounding natural plant communities, is rarely considered (Power & Mitchell 2004). However, pathogen mediated apparent competition has recently been shown to occur within grassland communities (Power & Mitchell 2004), and the proximity to crop hosts can be an important determinant of the prevalence of some strains of barley yellow dwarf virus in wild grasses (Power & Remold 1996). This provides strong evidence that spillover edge effects can occur in pathogen systems, and pathogen spillover may be an important process impacting wild plant populations (Gilbert & Hubbell 1996; Power & Mitchell 2004).

There are likely to be many additional examples of generalist natural enemies that can similarly benefit from cropping systems. Given the increasing dominance of agricultural habitats in modern landscapes, examining the implications of natural enemy spillover across agricultural–natural landscape boundaries is likely to be an important area of future research.

CONCLUSIONS

Despite the rarity of explicit studies on the topic, there are a number of reasons to predict that the spillover of insect natural enemies across cropland–natural habitat edges is likely to be a relatively common, and potentially important, process. First, a substantial body of literature illustrates that crop and natural habitats can share important insect natural enemies, and natural-enemy mediated edge effects have been documented within agroecosystems. Second, many cropping systems possess traits that are theoretically predicted to maximize system influences on adjacent habitats via subsidized consumer effects, including high productivity and temporally varying resource availability. These traits are predicted to promote the buildup and export of predators to surrounding natural landscapes, thereby increasing predation pressure near habitat edges. The magnitude and impact of spillover predation is predicted to be greatest when large differences in productivity occur between natural and cropland systems, and late in the growing season as resources within cropping systems decline. We conclude that the spillover of agriculturally subsidized insects has the potential to magnify predator impacts on native insect prey populations in habitat fragments. Such processes may be inimical to the maintenance of natural food-web structure in remnant habitats. Similar edge effects may result from the spillover of other groups of generalist natural enemies benefiting from cropland systems, such as insect herbivores, avian nest predators, mammalian seed predators and pathogens. We suggest that this understudied topic warrants increased experimental analysis and attention. More empirical work examining the prevalence and significance of natural enemy spillover will be critical to better understanding the effects of habitat loss on insect predator–prey interactions in increasingly agriculturally dominated landscapes.

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