

ISSUES IN AGRICULTURAL AND FOREST ENTOMOLOGY

Landscape structure, habitat fragmentation, and the ecology of insects

Mark D. Hunter

Institute of Ecology, University of Georgia, Athens, GA 30602-2202, U.S.A.

Introduction

My office doesn't have a window. If it did, and I could look across campus, my view would be a mosaic of buildings, grass, trees, parking areas, a couple of small streams, and even a lake. There are oak trees with diverse Cynipid assemblages, a myriad of arthropods in the litter beneath the ornamental plantings, and abundant pollinators on the *Hypericum* that lines the path from my office to the library. There are also diesel-belching buses and some insane planner's nightmare of one-way roads and dead-end footpaths. As a microcosm of the world at large, our campus is a study in fragmentation. Areas of natural, semi-natural, and grossly artificial vegetation are divided and subdivided into patches of various sizes in various degrees of isolation. Boundaries abound. A demented four-year-old with Lego[®] could not create a three-dimensional architecture this complex.

Yet within this fragmented landscape, insects persist in some abundance and diversity. As insect ecologists, we're obligated to understand the processes that influence the abundance, richness and diversity of insects in fragmented landscapes. As pest managers, we need to know how the architecture of landscapes influences pest population dynamics and their interactions with natural enemies and agents of control. As conservation biologists, we must develop strategies to maintain focal insect species, faunal diversity and the trophic interactions that drive key ecosystem processes. Whatever our entomological interests, landscape structure and habitat fragmentation have an influence on the ecology of the insects that we study.

If space is the final frontier of ecological theory (Kareiva, 1994), then fragmentation of space is the warp engine that drives research in spatial ecology. Critical issues such as local extinction of bird populations (Renjifo, 2001; Robinson *et al.*, 2001; Sekercioglu *et al.*, 2002), declining densities of small mammals and herpetofauna (Maisonneuve & Rioux, 2001), declines in pollinator bees due to deforestation (Brown & Albrecht, 2001; Cane, 2001) and the management of landscapes for insect biodiversity (Ehrlich & Murphy, 1987; Samways, 1992; Thomas, 1995; Di Giulio *et al.*, 2001) catch the imaginations of scientists and the public alike. There is

a growing sense of urgency and awareness that understanding the role of habitat fragmentation in ecological processes is a prerequisite for sound science, policy and management. Whether the goal is to predict the presence and abundance of species in fragmented landscapes (Cowley *et al.*, 2000), or to conserve species interactions and trophic structure (Fisher, 1998), the behavioural and dynamical responses of insects to landscape structure are key.

The features of landscapes that influence the population and community ecology of species, including insects, are well known. The ratio of habitat edge to interior (Chen *et al.*, 1995; Radeloff *et al.*, 2000), the isolation of habitat fragments (Collinge, 2000), patch area (Kruess & Tschardtke, 2000), patch quality (Hunter *et al.*, 1996; Kuussaari *et al.*, 2000; Hanski & Singer, 2001), patch diversity (Gathmann *et al.*, 1994; Varchola & Dunn, 2001) and microclimate (Braman *et al.*, 2000) all contribute to determining the abundance and richness of insects on landscapes. More recently, ecologists have incorporated temporal changes in landscape structure (Solbreck, 1995; Onstad *et al.*, 2001), genetic change in insect populations (Singer & Thomas, 1996; Ronce & Kirkpatrick, 2001), and differential responses of predators and prey (Kruess & Tschardtke, 1994; With *et al.*, 2002) into their understanding of the spatial ecology of insects. Even with a growing awareness of the features of landscapes that contribute to variation in insect populations and communities, there remain clear gaps in our understanding of the links between landscape change and insect dynamics. Below, I describe some of the recent work that has explored these links and suggest some approaches for future work.

Insect movement and habitat boundaries

Much can be learned about the impacts of fragmentation on insect populations by studying the movement of predators and prey among patch types in complex landscapes (Holland & Luff, 2000; Martin *et al.*, 2001; With *et al.*, 2002). Simple models assume that rates of movement are independent of landscape structure, typically assume constant movement rates whatever the landscape mosaic in question (Goodwin & Fahrig, 2002), and generally assume that dispersal is random (Conradt *et al.*, 2001). In reality, movement rates can vary markedly among features of the landscape such as edges and boundaries, and simple

Correspondence: Tel.: +1 706 542 1801; fax: +1 706 542 4819; e-mail: mhunter@sparc.ecology.uga.edu; website: <http://www.ecology.uga.edu/hunter.html>

diffusion models are unlikely to capture the movement of insects in fragmented habitats. For example, movement rates of the specialized goldenrod beetle, *Trirhabda borealis*, depend in part upon the patch structure of the environment within and among goldenrod fields (Goodwin & Fahrig, 2002). Similarly, the movement of carabid beetles within and among barley fields is reduced by the presence of hedgerows (Mauremooto *et al.*, 1995). Although it is well established that field boundaries can act as reservoirs of predator populations, particularly those of carabid and staphylinid beetles (Andersen, 1997), the opposing effects of hedgerows on increasing predator densities and decreasing rates of movement may have complex effects upon prey densities. The apparent permeability of some habitat boundaries (Duelli *et al.*, 1990) may be increased when beetles are hungry (Mauremooto *et al.*, 1995), suggesting that the physiological state of individuals will influence their movement among landscape features. Of course, landscape features themselves can influence the physiological condition of insects, including carabid beetles (Oestman *et al.*, 2001). It may be some time before we are able to incorporate 'insect health' into our understanding of landscape processes, but it is clear that the physiological condition of insects is both a product of landscape structure and a factor that influences responses to fragmentation. We need more studies that link insect physiology, landscape structure and rates of movement.

Of course, nothing is simple and not all boundaries are created equal in time or space (Varchola & Dunn, 1999). Particularly in agricultural systems, boundaries can vary from complex strips of woodland, through hedgerows, to roads and simple grassy edges. Varchola & Dunn (2001) report that the relative effects of woody and grassy boundaries around agricultural fields on predatory beetle richness and activity vary depending upon the time of year. Woody edges appear to be important for over-wintering beetle populations, whereas later in the growing season grassy and woody edges are about equally important. However, corridors and boundaries around agricultural fields can actually increase the densities of pest species and cause reductions in yield. In soybean agroecosystems, fields surrounded by uncultivated corridors have been shown to support higher pest densities, to suffer higher levels of defoliation and to produce lower yields (Kemp & Barrett, 1989). Similarly, the diversity of herbivorous insects within alfalfa fields is positively related to the length of woody border surrounding fields (Holland & Fahrig, 2000). In other words, measuring the activity and richness of predator populations in field boundaries may not provide an adequate prediction of their impacts upon herbivores and the subsequent crop losses that fields may suffer. Boundary effects upon insect herbivores may be variable at least in part because edges may actually be more suitable habitat for some herbivores. For example, forest tent caterpillars feeding within stands of sugar maple perform better in habitat edges than in habitat interior (Fortin & Mauffette, 2001). Trees on the edge of forests appear to produce foliage with higher concentrations of nitrogen and soluble sugars, both of which are positively correlated with insect performance. As forest fragmentation proceeds, and the ratio

of edge to interior rises, it is likely that the performance of forest tent caterpillars will improve.

If conservation, rather than pest management, is the focus of your research, then there seems little doubt that complex boundaries among habitat types can act to increase insect diversity. For example, riparian buffer strips at the side of lakes and streams seem to concentrate flying insects. In comparison to intact forest, Whitaker *et al.* (2000) reported higher densities of flying insects in riparian buffer strips, possibly because the strips collect airborne insects by acting as windbreaks. Higher concentrations of flying insects are associated with higher densities of insectivorous birds.

The matrix of unsuitable habitat between suitable habitat patches may have a profound influence on insect movement. In their studies of flea beetles, *Aphthona*, on leafy spurge, Jonsen *et al.* (2001) report that the quality of matrix habitat (grass vs. shrub) influences the ability of *A. nigricutis* to colonize patches of host plant. Given that leafy spurge is a weed pest, colonization by its biological control agents is of significant economic concern. Movement patterns varied between beetle sexes and between congeneric beetles, suggesting that there may be no simple relationship between matrix quality and the effectiveness of the biological control agents (Jonsen *et al.*, 2001). Variation among species in their responses to landscape structure and management practices seems to be a common feature of such studies (Banks, 1998; Zabel & Tschardtke, 1998; Braman *et al.*, 2000; Collinge, 2000; Di Giulio *et al.*, 2001).

Studying the movement of particular species among isolated patches is important, but a critical question remains; can fine-scale movement behaviours be used to predict broad scale patterns of distribution on heterogeneous landscapes? According to Jonsen & Taylor (2000), the answer may be yes. In their studies of damselflies in the genus *Calopteryx*, they have developed simulation models in which fine-scale movement behaviours were useful in predicting landscape-level distributions. It is true that the models required incorporating information on the architecture of the landscape, but it is nonetheless reassuring that measurements of specific behaviours can lead to accurate predictions of distribution patterns. Specifically, the probability of crossing patch boundaries and the rates of movement within given habitat patches were important determinants of damselfly distributions. Within the genus *Calopteryx*, movement rates are related to the realized connectivity of different landscape features but differ among species within the genus (Pither & Taylor, 1998), demonstrating that connectivity is as much a feature of the biology of species as it is the structure of landscapes. This last point has also been made by Haslett (2001) in a study of Dipteran diversity at landscape scales. From the 'fly point of view' borders that we perceive may be neutral to some Diptera, and border complexity may be a more relevant metric.

Patch size and isolation: differential effects upon predators and prey

Given the importance of movement to the spatial ecology of insects, it should be no surprise that the size and physical

arrangement of habitat patches on landscapes plays a fundamental role in determining the abundance and diversity of insect faunas. As in classic island biogeography theory (MacArthur & Wilson, 1967), patch area and patch isolation have often been associated with the richness of insect faunas (Kruess & Tscharrntke, 1994; Steffan-Dewenter & Tscharrntke, 2002). For example, Kruess & Tscharrntke (2000) report that the species richness of seed-feeding insects on bush vetch (*Vicia sepium*) increase with the area of meadows that contain the host plant, and decrease with isolation of the patch. The real contribution of Tscharrntke's group, however, has been to highlight the different spatial scales at which insect herbivores and natural enemies respond to patch structure. On bush vetch, the parasitoids of the seed-feeders suffered more from habitat loss and isolation than did their hosts. This suggests that the maintenance of higher trophic structure requires less fragmentation and isolation than does the maintenance of simple plant-insect assemblages (Kruess & Tscharrntke, 2000). Similarly, in a study of herbivores and predators in patches of nettle plants, herbivore populations were affected primarily by patch area, whereas predator populations were affected primarily by patch isolation (Zabel & Tscharrntke, 1998). The authors argue that maintaining connectivity is important to the maintenance of predator-prey interactions (Kruess & Tscharrntke, 1994). In their study of *Eucalyptus* remnants in grazed landscapes, Abensperg-Traun & Smith (1999) reported that predatory species of arthropod generally required larger habitat patches than did arthropods at lower trophic levels. Their data generally support the view of Tscharrntke's research group that predators are more vulnerable to fragmentation than are their prey. Ultimately, habitat fragmentation may lead to the truncation of food chains and the degradation of trophic structure. In old-growth forests in eastern Finland, for example, fragmentation reduces the richness of insect species associated with bracket fungi. Specifically, older fragments have a median food-chain length of one (only the fungus present), whereas large areas of old growth typically support food chains with three trophic levels (Komonen *et al.*, 2000). In my view, the realization that food-chain length and trophic structure are so vulnerable to fragmentation is the most important lesson that we have learned from studying insects on complex landscapes. It has profound implications for many fields of ecology, evolutionary biology and management.

Differential responses of predators and prey to landscape structure appear to hold when studies scale up to much larger areas. In a large-scale study of landscape structure and predator richness, Elliot *et al.* (1999) investigated the effects of landscape characteristics on the abundance and richness of predators of aphids in wheat fields in South Dakota. Using aerial photographs, they were able to demonstrate that increases in uncultivated land and increases in patchiness surrounding wheat fields were both associated with increasing abundance and richness in the predator communities within fields. Fragmentation, by decreasing the effectiveness of natural enemies, may therefore be associated with increases in the probability of insect outbreak. For example, the duration of forest tent

caterpillar, *Malacosoma disstria*, outbreaks in Canada increases in response to forest fragmentation (Roland, 1993). Effects of fragmentation on both parasitoids (Roland & Taylor, 1997) and disease (Roland & Kaupp, 1995) have been implicated in their dynamics under landscape change. Finally, the age of habitat fragments may also influence both the occurrence of herbivores and their probability of parasitism (Athen & Tscharrntke, 1999). Such age effects call for the inclusion of temporal patch structure into our understanding of insect ecology in fragmented habitats.

Because this is ecology, exceptions do exist to the general relationships between patch area, patch isolation and species richness. For example, populations of pollinating bees seem much more attuned to the quality of patches than to their area or isolation (Gathmann *et al.*, 1994; Tscharrntke *et al.*, 1998). In fact, for pollinators, management regimes that focus upon floral diversity appear to have a greater effect than those related to the arrangement of patches on the landscape, and the mobility of insect pollinators may make them less susceptible to fragmentation than some other insect groups (Cane, 2001). Nonetheless, concerns remain that fragmentation may adversely affect particular species of native pollinators. In Argentinean subtropical dry forest, for example, fragmentation reduces visitation by native bees but increases visitation by exotic honey bees (Aizen & Feinsinger, 1994). The perceived severity of fragmentation effects therefore depend upon whether the focus is on conservation of native species or on the ecosystem service of pollination. Finally, small and dispersed habitat fragments are known to increase beta diversity across some landscapes. Tscharrntke *et al.* (2002) emphasize the importance of small habitat fragments for certain insect species and point out that, at least for some butterfly groups, small fragments support more species than do equivalent areas in large patches. For conservation purposes, they recommend a combination of large patches with scattered small fragments to maximize beta diversity.

Given the effects of habitat fragmentation and isolation on predator-prey interactions, we might expect that landscape structure should play a role in the effectiveness of biological control. However, most recent studies of interactions between landscape features and pest management have focused upon habitat heterogeneity rather than area or isolation *per se*. For example, rates of parasitism of armyworm larvae are higher in complex agricultural landscapes than in simple landscapes (Marino & Landis, 1996). Similarly, parasitism of rape pollen beetles declines significantly with distance from field margins (Tscharrntke *et al.*, 2002). Complex landscapes may provide a diversity of basal resources that supplement populations of predators. This appears to occur in Indonesian rice fields, where the availability of detritus acts to supplement the food web and maintain high populations of generalist predators that suppress rice pests (Settle *et al.*, 1996). Similarly, mulching of agricultural fields in southern Sweden has been shown to increase the densities of staphylinid beetles (Raemert *et al.*, 2001). However, relationships between pest damage and landscape structure are not simple. In some cases, there appear to be few changes in species richness along gradients

of agricultural intensification (Burel *et al.*, 1998) and, in at least one case, the richness of the insect community in agricultural fields actually increased with patch isolation (Fahrig & Jonsen, 1998). Some generalist spiders appear to exhibit preferences for agricultural habitat over less-disturbed habitat (Downie *et al.*, 2000) and the degree of polyphagy of both predators and pests is likely to influence their response to changes in landscape structure (Jonsen & Fahrig, 1997). The bottom line is that complex landscapes beget complex interactions and it will require some clever manipulative experiments to untangle the often confounding effects of boundary quantity, boundary quality, matrix habitat, patch area and patch isolation on the biological control of insect pests.

Corridors and connectivity

It has become a textbook paradigm that habitat corridors that connect isolated habitat patches will increase the abundance and diversity of species within those patches through increases in rates of immigration. How depressing, then, that there exist so few experimental studies in which both patch isolation and the presence of corridors have been manipulated to dissect their relative effects upon insect communities. In one such study (Collinge, 2000), the presence of corridors had relatively weak effects upon species loss and colonization of isolated patches by insects in native grassland. Weak effects of corridors on species richness were detected in medium-sized patches, but there were no overall effects upon rates of colonization. Critically, recolonization of patches by rare species was unaffected by the presence or absence of corridors. Variation in corridor effects among species and among years suggests that there exist few consistent effects of habitat corridors in this grassland system. Variability in the value of corridors seems to be a feature of the few careful studies that have been conducted. For example, in his exploration of movement by the butterfly *Junonia coenia*, Haddad (2000) reported that corridors promoted colonization of patches when butterflies were released at long distances from suitable habitat. At shorter distances, however, corridors were not effective at promoting colonization. Nonetheless, movement of butterflies among patches was significantly enhanced by the presence of corridors (Haddad, 1999a) and population densities were higher in connected patches than in isolated patches of similar area (Haddad & Baum, 1999). Haddad's (1999b) simulation models suggest that the movement behaviour of butterflies at patch-edge boundaries can be used to predict the effects of corridors on movement among patches. To be honest, there are simply too few experimental studies of corridor effects on insects to draw many conclusions at present. The only conclusion that I can draw is that we need to do more.

Metapopulation dynamics

Because of its focus upon the dynamics of single species occupying discrete patches of habitat, the concept of metapopulation dynamics has much to offer in studies of habitat

fragmentation. Species living in highly fragmented landscapes often occur as metapopulations, in which local populations turn over quite frequently, but the metapopulation (the population of populations) tends to persist (Levins, 1969; Ehrlich & Murphy, 1987; Hanski, 1999). The rate of population turnover is generally related to factors such as population size and connectivity. However, patch quality may also be an important determinant of patch colonization and persistence (Hanski & Singer, 2001). For example, the Glanville fritillary butterfly, *Melitaea cinxia*, in Finland occurs in discrete habitat patches that contain two potential host-plant species, *Plantago lanceolata* and *Veronica spicata* (Kuussaari *et al.*, 2000). The probability of an empty patch being colonized depends in part upon the perceived quality of that patch by ovipositing female butterflies. Colonization rates increase when surrounding patches contain butterflies that have experienced similar host-plant composition, suggesting that the prior experience of local butterflies influences their perception of habitat quality and their probability of colonizing a new patch (Hanski & Singer, 2001). Patch quality can also influence emigration rates. For example, emigration of the frugivorous butterfly, *Hamadryas februa*, from islands in Venezuela has been linked to the availability of suitable host-plant species (Shahabuddin *et al.*, 2000). The incorporation of patch quality and female preference into studies of metapopulations represents a significant advance in the field and adds a level of reality to dynamics that was missing in earlier metapopulation studies (Hunter *et al.*, 1996, 2000).

Of course, issues of patch quality are central to complementary theories of insect population dynamics in fragmented landscapes, such as theories of source–sink dynamics (Pulliam, 1988). Source–sink dynamics are based upon high quality patches (births exceed deaths, emigration exceeds immigration) supporting populations in low quality patches (deaths exceed births, immigration exceeds emigration), so extending the distribution of organisms in space. As Boughton (1999) has pointed out, changes in patch quality and in rates of movement can result in interesting reversals in the status of sources and sinks. In other words, by focusing upon the quality of patches and the net movement of organisms, source–sink theory is sufficiently robust to incorporate the temporal changes in landscape structure that characterize our changing world.

Using metapopulation or source–sink concepts, pest managers may be able to manipulate patch structure in time and space to influence the dynamics of pest species (Ives & Settle, 1997). Given their current place in conservation biology, it is ironic that metapopulation models were developed originally for pest management rather than species conservation (Levins, 1969). Uses of metapopulation theory in the arrangement of crop patches and in the timing of crop rotations have yet to realize their potential in pest management, perhaps because of the necessity of region-wide cooperation in the placement and rotation of crops (Helenius, 1997). Moreover, there exists potential conflict between metapopulation strategies that aim to reduce pest populations and those that aim to increase predator populations (Ives & Settle, 1997).

The form and value of habitat patches in complex landscapes can vary dramatically over time (Solbreck, 1995), yet we know relatively little about the effects of temporal changes in spatial structure on insect populations. Much of what we do know about temporal effects of landscape change comes from studies of insect pests and predators under crop rotation. Crop rotation has traditionally been effective in reducing the damage by insect pests to particular crops. However, Onstad *et al.* (2001) have shown that frequent rotation may select for behavioural changes that ameliorate the negative impacts of landscape change on insect dynamics. Depending upon the diversity of the landscape and the frequency of rotation, selection may act to change patterns of movement or feeding preferences that mitigate the effects of landscape change. There is little doubt that adaptation is a pervasive evolutionary response to changing landscape features (Singer & Thomas, 1996). As Ronce & Kirkpatrick (2001) point out, even small changes in connectivity between two habitats can result in a 'migrational meltdown', during which population sizes drop and specialization on a single habitat-type evolves. Their models of the evolution of habitat generalists and habitat specialists suggest that migration rates, and hence connectivity, are critical to evolutionary change in heterogeneous landscapes (Ronce & Kirkpatrick, 2001) and may explain some patterns of genetic variation among insect populations in space (Kuussaari *et al.*, 2000; Wilcock *et al.*, 2001). Lack of movement and increasing specialization in local habitat patches has been implicated as a cause of inbreeding depression in some butterfly metapopulations (Haikola *et al.*, 2001). There is even evidence that fragmentation can select for variation in dispersal abilities within species. For example, wing lengths, wing widths and thoracic weights of the forest damselfly *Calopteryx maculata* vary between populations along forested streams and those along streams through pastures (Taylor & Merriam, 1995). Selection appears to have increased flight ability within populations in fragmented pasture habitats. In fact, selection for strong dispersal ability, whatever its cause, is likely to reduce the impact of fragmentation upon the dynamics of insect species. The dynamics of some grass-feeding insects, for example, are dominated by the ephemeral availability of new grass shoots, and their dispersal abilities reflect the necessity of finding resources that vary markedly in space and time. As a consequence, their populations appear to be less affected by habitat fragmentation than those of some other herbivores (Dubbart *et al.*, 1998).

What's missing?

I have already mentioned a few areas of research that would benefit from further work, including an accurate assessment of corridor effects on insects (Collinge, 2000; Haddad, 2000), and the development of links among insect physiology, rates of movement and landscape structure. There are many others. First, it would be worthwhile to develop some rigorous and standard descriptions of both the processes of landscape change and the structures that result. The development of landscape mosaics is actually more complicated

than the simple processes of fragmentation or change in land use. Collinge & Forman (1998) suggest that there are at least four processes that contribute to the generation of landscape mosaics; shrinkage, bisection, fragmentation and perforation. By subdividing mosaic formation in this way, Collinge & Forman (1998) were able to show that, in grassland habitats, shrinkage results in a decline in insect species richness, whereas fragmentation actually increases species richness. Whatever 'taxonomy' of landscape structure that we develop, a common language and standard methods would go far in promoting synthesis among disparate studies (Duelli *et al.*, 1999).

Second, we need to strike a balance between correlative and mechanistic approaches. Manipulative experiments are ideal for studying patterns of movement and other critical population rates at local scales. They are invaluable for understanding the complexities of mosaic formation and dissecting out covariation among landscape traits (Banks, 1998; Collinge & Forman, 1998; Golden & Crist, 2000). However, we also need more emphasis on research at larger spatial scales (Steffan-Dewenter & Tschardt, 2002), which will undoubtedly rely in part on correlations and modelling. By combining both experimental approaches at local scales and correlative approaches across larger scales, it may be possible to explain some of the inconsistencies that occur in the literature. For example, populations of jack pine budworm (*Choristoneura pinus pinus*) are positively correlated with the density of habitat edge during population increase, but negatively correlated with the same landscape feature during population decrease (Radeloff *et al.*, 2000). This contradictory result will only be explained by studies of mechanism at the local level.

Third, we need to make much more use of the historical data that are available to us. Both amateur and professional entomologists have generated a plethora of records on the distribution and abundance of species over many decades of collecting. In combination with historical records of land use change, such data should provide us with considerable insight into how past landscape change has influenced our current insect fauna and how future change may affect it further. Using insect fossils, we can delve back even further and explore the fascinating long-term changes in insect fauna recorded in the fossil record (Schwert, 1996). For example, in north-eastern Iowa, the beetle fauna prior to Euro-American settlement was characterized by a diverse assemblage of carabids (terrestrial) and elmids (aquatic). After settlement and intensive cultivation, the dominant fauna has been replaced by weed and crop weevils and by dung beetles, with degradation of the aquatic elmids. The changes in north-eastern Iowa parallel changes in British sites during the late Bronze age where, 2100 years ago, insect faunas were affected by the transformation of natural landscapes to agrarian use (Schwert, 1996).

Finally, we need to explore in much greater detail the effects of landscape change and habitat fragmentation on ecological interactions. We have learned a considerable amount by studying landscape effects on the abundance of species and the richness of communities. However, the most profound effects of habitat fragmentation may result from

changes in interactions among species. For example, the loss of keystone species in communities may result in cascading effects through trophic webs that ultimately influence ecosystem processes (Tschardtke, 1992; Didham *et al.*, 1996; Fisher, 1998; Komonen *et al.*, 2000; Gibbs & Stanton, 2001). We need to know the general effects that losses in insect biomass have on higher trophic levels such as insectivorous birds (Van Wilgenburg *et al.*, 2001). We need to explore the interactive effects of multiple environmental changes such as global warming (Hill *et al.*, 1999) or species invasions (Toft *et al.*, 2001) along with habitat fragmentation. Invasion by the weed *Tradescantia fluminensis* into fragmented forests in New Zealand has caused a decline in fungus fly and beetle diversity in the forest understorey (Toft *et al.*, 2001), presumably because of replacement of the natural forest flora. This is a clear example of two interacting factors – fragmentation and the invasion of exotics – influencing trophic dynamics within forests. Insects dwell within complex ecosystems and interact with other taxonomic groups and the abiotic environment. The true effects of landscape change and fragmentation upon the ecology of insects will only be understood by embracing the ecological complexity that characterizes the world within which insects live.

Acknowledgements

I thank the National Science Foundation (Grant DEB-9906366) for supporting our work on habitat gradients and the population dynamics of insect herbivores.

References

- Abensperg-Traun, M. & Smith, G.T. (1999) How small is too small for small animals? Four terrestrial arthropod species in different-sized remnant woodlands in agricultural Western Australia. *Biodiversity and Conservation*, **8**, 709–726.
- Aizen, M.A. & Feinsinger, P. (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine 'Chaco Serrano'. *Ecological Applications*, **4**, 378–392.
- Andersen, A. (1997) Densities of overwintering carabids and staphylinids. *Journal of Applied Entomology*, **121**, 77–80.
- Athen, O. & Tschardtke, T. (1999) Insect communities of *Phragmites* habitats used for sewage purification: effects of age and area of habitats on species richness and herbivore–parasitoid interactions. *Limnologia. Jena*, **29**, 71–74.
- Banks, J.E. (1998) The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. *Oecologia*, **117**, 239–246.
- Boughton, D.A. (1999) Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. *Ecology*, **80**, 2727–2739.
- Braman, S.K., Latimer, J.G., Oetting, R.D., McQueen, R.D., Eckberg, T.B. & Prinster, M. (2000) Management strategy, shade, and landscape composition effects on urban landscape plant quality and arthropod abundance. *Journal of Economic Entomology*, **93**, 1464–1472.
- Brown, J.C. & Albrecht, C. (2001) The effect of tropical deforestation on stingless bees of the genus *Melipona* (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. *Journal of Biogeography*, **28**, 623–634.
- Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., Thenail, C., Brunel, E. & Lefeuvre, J.-C. (1998) Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologia*, **19**, 47–60.
- Cane, J.H. (2001) Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology*, **5**, U149–U161.
- Chen, J., Franklin, J.F. & Spies, T.A. (1995) Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications*, **5**, 74–86.
- Collinge, S.K. (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. *Ecology*, **81**, 2211–2226.
- Collinge, S.K. & Forman, R.T.T. (1998) A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos*, **82**, 66–84.
- Conradt, L., Roper, T.J. & Thomas, C.D. (2001) Dispersal behavior of individuals in metapopulations of two British butterflies. *Oikos*, **95**, 416–424.
- Cowley, M.J.R., Wilson, R.J., Leon-Cortes, J.L., Gutierrez, D., Bulman, C.R. & Thomas, C.D. (2000) Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *Journal of Applied Ecology*, **37**, 60–72.
- Di Giulio, M., Edwards, P.J. & Meister, E. (2001) Enhancing insect diversity in agriculture grasslands: the roles of management and landscape structure. *Journal of Applied Ecology*, **38**, 310–319.
- Didham, R.K., Ghazoul, J., Stork, N.E. & Davis, A.J. (1996) Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution*, **11**, 255–260.
- Downie, I.S., Ribera, I., McCracken, D.I., Wilson, W.L., Foster, G.N., Waterhouse, A., Abernethy, V.J. & Murphy, K.J. (2000) Modelling populations of *Erigone atra* and *E. dentipalis* (Araneae: Linyphiidae) across an agriculture gradient in Scotland. *Agriculture, Ecosystem and Environment*, **80**, 15–28.
- Dubbert, M., Tschardtke, T. & Vidal, S. (1998) Stem-boring insects of fragmented *Calamagrostis* habitats: herbivore-parasitoid community structure and the unpredictability of grass shoot abundance. *Ecological Entomology*, **23**, 271–280.
- Duelli, P., Obrist, M.K. & Schmatz, D.R. (1999) Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture, Ecosystems and Environment*, **74**, 33–64.
- Duelli, P., Studer, M., Marchand, I. & Jacob, S. (1990) Population movements of arthropods between natural and cultivated areas. *Biological Conservation*, **54**, 193–207.
- Ehrlich, P.R. & Murphy, D.D. (1987) Conservation lessons from long-term studies of checkerspot butterflies. *Conservation Biology*, **1**, 122–131.
- Elliot, N.C., Kieckhefer, R.W., Lee, J.H. & French, B.W. (1999) Influence of within-field and landscape factors on aphid predator populations in wheat. *Landscape Ecology*, **14**, 239–252.
- Fahrig, L. & Jonsen, I. (1998) Effect of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. *Ecosystems*, **1**, 197–205.
- Fisher, B.L. (1998) Insect behavior and ecology in conservation: preserving functional species interactions. *Annals of the Entomological Society of America*, **91**, 155–158.
- Fortin, M. & Mauffette, Y. (2001) Forest edge effects on the biological performance of the forest tent caterpillar (Lepidoptera: Lasiocampidae) in sugar maple stands. *Ecoscience*, **8**, 164–172.
- Gathmann, A., Greiler, H.J. & Tschardtke, T. (1994) Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia*, **98**, 8–14.

- Gibbs, J.P. & Stanton, E.J. (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. *Ecological Applications*, **11**, 79–85.
- Golden, D.M. & Crist, T.O. (2000) Experimental effects of habitat fragmentation on rove beetles and ants: patch area or edge? *Oikos*, **90**, 525–538.
- Goodwin, B.J. & Fahrig, L. (2002) Effect of landscape structure on the movement behavior of a specialized goldenrod beetle, *Trirhabda borealis*. *Canadian Journal of Zoology*, **80**, 24–35.
- Haddad, N.M. (1999a) Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications*, **9**, 612–622.
- Haddad, N.M. (1999b) Corridor use predicted from behaviors at habitat boundaries. *American Naturalist*, **153**, 215–227.
- Haddad, N.M. (2000) Corridor length and patch colonization by a butterfly, *Junonia coenia*. *Conservation Biology*, **14**, 738–745.
- Haddad, N.M. & Baum, K.A. (1999) An experimental test of corridor effects on butterfly densities. *Ecological Applications*, **9**, 623–633.
- Haikola, S., Fortelius, W., O'Hara, R.B., Kuussaari, M., Wahlberg, N., Saccheri, I.J., Singer, M.C. & Hanski, I. (2001) Inbreeding depression and the maintenance of genetic load in *Melitaea cinxia* metapopulations. *Conservation Genetics*, **2**, 325–335.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hanski, I. & Singer, M.C. (2001) Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. *American Naturalist*, **158**, 341–353.
- Haslett, J.R. (2001) Biodiversity and conservation of *Diptera* in heterogeneous land mosaics: a fly's eye view. *Journal of Insect Conservation*, **5**, 71–75.
- Helenius, J. (1997) Spatial scales in ecological pest management (EPM): importance of regional crop rotations. *Biological Agriculture and Horticulture*, **15**, 163–170.
- Hill, J.K., Thomas, C.D. & Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **266**, 1197–1206.
- Holland, J. & Fahrig, L. (2000) Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. *Agriculture, Ecosystems and Environment*, **78**, 115–122.
- Holland, J.M. & Luff, M.L. (2000) The effects of agricultural practices on Carabidae in temperate agroecosystems. *Integrated Pest Management Review*, **5**, 109–129.
- Hunter, M.D., Forkner, R.E. & McNeil, J.N. (2000) Heterogeneity in plant quality and its impact on the population ecology of insect herbivores. *The Ecological Consequences of Environmental Heterogeneity* (ed. by M. A. Hutchings, E. A. John and A. J. A. Stewart), pp. 155–179. Blackwell Science, Oxford.
- Hunter, M.D., Malcolm, S.B. & Hartley, S.E. (1996) Population-level variation in plant secondary chemistry and the population biology of herbivores. *Chemoecology*, **7**, 45–56.
- Ives, A.R. & Settle, W.H. (1997) Metapopulation dynamics and pest control in agricultural systems. *American Naturalist*, **149**, 220–246.
- Jonsen, I.D., Bouchier, R.S. & Roland, J. (2001) The influence of matrix habitat on *Aphanta* flea beetle immigration to leafy spurge patches. *Oecologia*, **127**, 287–294.
- Jonsen, I.D. & Fahrig, L. (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology*, **12**, 185–197.
- Jonsen, I. & Taylor, P.D. (2000) *Calopteryx* damselfly dispersions arising from multiscale response to landscape structure. *Conservation Ecology*, **4**, 57–76.
- Kareiva, P.M. (1994) Space: the final frontier for ecological theory. *Ecology*, **75**, 1.
- Kemp, K.C. & Barrett, G.W. (1989) Spatial patterning: impact of uncultivated corridor on arthropod populations within soybean agroecosystems. *Ecology*, **70**, 114–128.
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000) Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, **90**, 119–126.
- Kruess, A. & Tscharnkte, T. (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia*, **122**, 129–137.
- Kruess, A. & Tscharnkte, T. (1994) Habitat fragmentation, species loss, and biological control. *Science*, **264**, 1581–1584.
- Kuussaari, M., Hanski, I. & Singer, M. (2000) Local speciation and landscape-level influence on host use in an herbivorous insect. *Ecology*, **81**, 2177–2187.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Maisonnette, C. & Rioux, S. (2001) Importance of riparian habitats for small mammal and herpetofaunal communities in agricultural landscapes of southern Quebec. *Agriculture, Ecosystems and Environment*, **83**, 165–175.
- Marino, P.C. & Landis, D.A. (1996) Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications*, **6**, 276–284.
- Martin, M., Bastardie, F., Richard, D. & Burel, F. (2001) Studying boundary effects on animal movement in heterogeneous landscapes: the case of *Abax ater* (Coleoptera: Carabidae) in hedgerow network landscapes. *Comptes Rendus de l'Académie des Sciences*, **324**, 1029–1035.
- Mauremooto, J.R., Wratten, S.D., Worner, S.P. & Fry, G.L.A. (1995) Permeability of hedgerows to predatory carabid beetles. *Agriculture, Ecosystems and Environment*, **52**, 141–148.
- Oestman, O.E., Bengtsson, J., Weibull, A.C. & Ekbom, B. (2001) Landscape complexity and farming practice influence the condition of polyphagous carabid beetles. *Ecological Applications*, **11**, 480–488.
- Onstad, D.W., Spencer, J.L., Guse, C.A., Levine, E. & Isard, S.A. (2001) Modeling evolution of behavioral resistance by an insect to crop rotation. *Entomologia Experimentalis et Applicata*, **100**, 195–201.
- Pither, J. & Taylor, P.D. (1998) An environmental assessment of landscape connectivity. *Oikos*, **83**, 166–174.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.
- Radeloff, V.C., Mladenoff, D.J. & Boyce, M.S. (2000) The changing relation of landscape patterns and jack pine budworm populations during an outbreak. *Oikos*, **90**, 417–430.
- Raemert, B., Ehnstroem, B. & Lundberg, S. (2001) Effects of mulching and intercropping on occurrence of ground beetles and rove beetles (Coleoptera: Carabidae and Staphylinidae) in carrot cultivations. *Entomologisk Tidskrift*, **122**, 177–187.
- Renjifo, L.M. (2001) Effect of natural and anthropogenic landscape matrices on the abundance of sub-Andean bird species. *Ecological Applications*, **11**, 14–31.
- Robinson, R.A., Wilson, J.D. & Crick, H.Q.P. (2001) The importance of arable habitat for farmland birds in grassland landscapes. *Journal of Applied Ecology*, **38**, 1059–1069.
- Roland, J. (1993) Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, **93**, 25–30.

- Roland, J. & Kaupp, W.J. (1995) Reduced transmission of forest tent caterpillar (Lepidoptera; Lasiocampidae) nuclear polyhedrosis virus at the forest edge. *Environmental Entomology*, **24**, 1175–1178.
- Roland, J. & Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, **386**, 710–713.
- Ronce, O. & Kirkpatrick, M. (2001) When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution*, **55**, 1520–1531.
- Samways, M.J. (1992) Some comparative insect conservation issues in north temperate, tropical, and south temperate landscapes. *Agriculture, Ecosystems and Environment*, **40**, 137–154.
- Schwert, D.P. (1996) Effect of Euro-American settlement on an insect fauna. *Annals of the Entomological Society of America*, **89**, 53–63.
- Sekercioglu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D. & Sandi, R.F. (2002) Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences, USA*, **99**, 263–267.
- Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A.S., Pajarningsih & Sartanto. (1996) Managing tropical pests through conservation of generalist natural enemies and alternative prey. *Ecology*, **77**, 1975–1988.
- Shahabuddin, G., Herzner, G.A., Aponte, R. & Gomez, M.C. (2000) Persistence of a frugivorous butterfly species in Venezuelan forest fragments: the role of movement and habitat quality. *Biodiversity and Conservation*, **9**, 1623–1641.
- Singer, M.C. & Thomas, C.D. (1996) Evolutionary responses of a butterfly metapopulation to human- and climate-caused environmental variation. *American Naturalist*, **148**, S9–S39.
- Solbreck, C. (1995) Variable fortunes in a patchy landscape – the habitat templet of an insect migration. *Researches on Population Ecology*, **37**, 129–134.
- Steffan-Dewenter, I. & Tscharntke, T. (2002) Insect communities and biotic interactions on fragmented calcareous grasslands: a mini review. *Biological Conservation*, **104**, 275–284.
- Taylor, P.D. & Merriam, G. (1995) Wing morphology of a forest damselfly is related to landscape structure. *Oikos*, **73**, 43–48.
- Thomas, J.A. (1995) Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. *Ibis*, **137**, S112–S119.
- Toft, R.J., Harris, R.J. & Williams, P.A. (2001) Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand. *Biological Conservation*, **102**, 31–46.
- Tscharntke, T. (1992) Fragmentation of *Phragmites* habitats, minimum viable population size, habitat suitability, and local extinction of moths, midges, flies, aphids, and birds. *Conservation Biology*, **6**, 530–536.
- Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, **35**, 708–719.
- Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, **12**, 354–363.
- Van Wilgenburg, S.L., Mazerolle, D.F. & Hobson, K.A. (2001) Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. *Ecoscience*, **8**, 454–461.
- Varchola, J.M. & Dunn, J.P. (1999) Changes in ground beetle (Coleoptera: Carabidae) assemblages in farming systems bordered by complex or simple roadside vegetation. *Agriculture, Ecosystems and Environment*, **73**, 41–49.
- Varchola, J.M. & Dunn, J.P. (2001) Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. *Agriculture, Ecosystems and Environment*, **83**, 153–163.
- Whitaker, D.M., Carroll, A.L. & Montevecchi, W.A. (2000) Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. *Canadian Journal of Zoology*, **78**, 740–747.
- Wilcock, H.R., Hildrew, A.G. & Nichols, R.A. (2001) Genetic differentiation of a European caddisfly: past and present gene flow among fragmented larval habitats. *Molecular Ecology*, **10**, 1821–1834.
- With, K.A., Pavuk, D.M., Worchuck, J.L., Oates, R.K. & Fisher, J.L. (2002) Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications*, **12**, 52–65.
- Zabel, J. & Tscharntke, T. (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differently? *Oecologia*, **116**, 419–425.

Accepted 30 May 2002

Habitat diversity affects the structure and mechanisms of species coexistence in biotic communities because different species. *J Biodivers Endanger Species*, an open access journal ISSN: 2332-2543. A continuing challenge in ecology is disentangling the relative role of deterministic processes from chance, historical factors in structuring ecological communities [3,4,26]. Many ecological models of local species interactions in a community predict the occurrence of priority effects due to alternative stable equilibrium [27]. For example, [29] noted that low levels of habitat and landscape fragmentation may result in ill-functioning communities while greater fragmentation may result in species losses and ultimately in the loss of whole communities. Habitat fragmentation and dispersal ability are the driving forces behind the regional persistence of parasitoid populations (Hanski and Gilpin, 1997; Hassell et al., 1991). The population dynamics of such systems are highly variable and depend on species characteristics and landscape organization (Tschamntke and Brandl, 2004). Spatial ecology studies have identified diverse responses of populations to habitat loss and fragmentation. A classical metapopulation (sensu Levins, 1969) is one of several spatial population structures that may emerge. Others include mainland-island metapopulations (Pulliam, 1988), ephemeral aggregations of individuals, isolated populations, and synchronized local populations (Hirzel et al., 2007). Hirzel et al. Habitat fragmentation and landscape change. Andrew F. Bennett and Denis A. Saunders. Broad-scale destruction and fragmentation of native vegetation is a highly visible result of human land-use throughout the world (Chapter 4). From the Atlantic Forests of South America to the tropical forests of Southeast Asia, and in many other regions on Earth, much of the original vegetation now remains only as fragments amidst expanses of land committed to feeding and housing. Litter decomposition and nutrient cycling, and the structure and composition of vegetation. Changes to biophysical processes from land Habitat fragmentation describes the emergence of discontinuities (fragmentation) in an organism's preferred environment (habitat), causing population fragmentation and ecosystem decay. Causes of habitat fragmentation include geological processes that slowly alter the layout of the physical environment (suspected of being one of the major causes of speciation), and human activity such as land conversion, which can alter the environment much faster and causes the extinction of many species. More Ecologists agree that habitat destruction is detrimental to the maintenance of biodiversity, but they disagree often strongly on the extent to which fragmentation itself is to blame (4, 5). Early hypotheses based on the biogeography of oceanic islands (6) provided a theoretical framework to understand fragmentation's effect on extinction in terrestrial landscapes composed of islands of natural habitat scattered across a sea. Long-term experiments are a powerful tool for understanding the ecological consequences of fragmentation (20). Whereas observational studies of fragmented landscapes have yielded important insights (9, 21), they typically lack rigorous controls, replication, randomization, or baseline data.

Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology* 4: 150–166. Land, EISSN 2073-445X, Published by MDPI Disclaimer. The statements, opinions and data contained in the journal Land are solely those of the individual authors and contributors and not of the publisher and the editor(s). MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations. RSS Content Alert. Further Information. 3. 200 International dimensions of landscape ecology. . Volume 02. 3. 137--138 Advance regeneration and seed banking of woody plants in Ohio pine plantations: Implications for landscape change.Â 1. 69--80 Habitat corridors and the conservation of small mammals in a fragmented forest environment. Andrew F. Bennett;. Volume 04.Â 3. 147--159 Effect of landscape structure and dynamics on species diversity in hedgerow networks. Françoise Burel;. Volume 06. Future developments in the application of island biogeography principles to urban insect conservation should address temporal trends in species persistence and the analysis of species co-occurrence and nestedness. Keywords. arthropods conservation biology equilibrium theory green infrastructure islands species richness urbanization urban parks.Â Delgado de la flor, Yvan A. Perry, Kayla I. Turo, Katherine J. Parker, Denisha M. Thompson, Jennifer L. Gardiner, Mary M. and Smith, Annabel 2020. Local and landscape-scale environmental filters drive the functional diversity and taxonomic composition of spiders across urban greenspaces. *Journal of Applied Ecology*, Vol. 57, Issue. 8, p. 1570.