Landscape woody border increases insect diversity in alfalfa fields

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Abstract

Predicting the overall effect of woody borders on insect assemblages in agricultural landscapes is difficult because the effects that they have been hypothesized to have are numerous, and often conflicting. Management decisions are further complicated because the aims of insect conservation and agricultural production may often conflict. Results of four studies carried out on insects in alfalfa fields using different methods are discussed. The results of these studies suggest that woody borders can increase insect richness without a cost to agricultural production.

Introduction

Fencerows in North America have typically been formed from areas being cleared for agriculture with linear remnants of earlier continuous forest left between them, or by trees growing up along fences, stone piles and other features between fields. In this way their formation and structure is different from the hedgerows of Europe, which are frequently planted, and often tended. Much more research has been done on woody borders in Europe than in North America. Despite these differences however, the literature shows that much research has focused on the same questions in Europe and North America. For the purposes of this paper we use the term woody border to refer to both hedgerows and fencerows, and the term field margin to refer more generally to margins with or without woody vegetation.

Fencerows have been suggested to be important in the conservation of many different taxa, including insects, small mammals, and birds. The fate of fencerows however, will probably be determined by the effect that they have on agriculture through insects. In this paper we review some of the ways in which woody borders may have an impact on the assemblages of insects found in agricultural areas. We look at the results of four studies carried out by members of the Landscape Ecology laboratory at Carlton University examining insect assemblages in alfalfa (*Medicago sativa* L.) fields and discuss what the results show about the impact of woody borders. Finally we discuss these results in light of previous work, and what this tells us about the use of woody borders for insect conservation and pest control.

Insect conservation through fencerows

Woody borders increase the structural and vegetation diversity in agricultural areas. For insects in these areas, field margins can be a source of increased habitat diversity (Morris & Webb, 1987). Thomas and Marshall (1999) found a correlation between arthropod diversity and floral diversity of field margins. Several studies have found greater insect diversity in

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hedgerows than in agricultural fields (Lewis, 1969; Bowden & Dean, 1977). This increase in diversity has been found to be consistent across a range of scales beyond the woody border itself. Dennis and Fry (1992) found increased insect richness in the part of the field adjacent to a hedgerow. Holland and Fahrig (2000) found an increase in insect family richness in fields situated in landscapes with more woody borders within 1km of the field than in fields with less woody border in the landscape. The consistency of these results is a strong argument for the conservation potential of woody borders.

Insect conservation must be concerned with more than simply maximizing species richness. If we wish to preserve native habitats and species it may be important to see to what extent woody borders can aid in preserving species which inhabited the forest habitat that has largely been cleared for agriculture. This is not to suggest that woody borders can replace forest patches as refuges for these species. Studies have shown that forests and fencerows differ in structure and vegetation species (Fritz & Merriam, 1994, 1996), and in carabid beetle assemblages (Fournier & Loreau, 2001). Woody borders may however be important in providing dispersal opportunities for some forest species (Burel & Baudry, 1995). This would help maintain the species in the landscape through rescue effect (Brown & Kodric-Brown, 1977) and recolonization of local extinctions. The ability of field margins to contribute to such processes through dispersal depends on limiting the disturbances, such as grazing, within these margins (Charrier *et al.*, 1997; Petit & Usher, 1998). The presence of woody vegetation could be important in providing protection from such disturbances if, for example, they limit access to the margin by grazing mammals.

Entomophagous insects and woody borders

The enhancement of insect predator species' populations is one of the most commonly invoked reasons for the preservation of woody borders around crop fields (ex: Dennis and Fry, 1992; Dennis & Wratten, 1991; Hart *et al.*, 1994; Sustek, 1992; Wratten, 1988). These studies have found that field margin habitats contribute to both the density and diversity of predacious species (Coombs & Sotherton, 1986; Kromp, 1999; Sotherton, 1985). Field margins are considered important in providing complementary habitat in the rich carabid beetle literature that shows these species over-wintering in sheltered field borders and foraging in adjacent crop fields (Wratten & Thomas, 1990; Thomas *et al.*, 1998). Therefore the margins increase biodiversity and help to increase predator insects. However, there has been recent concern expressed regarding the lack of empirical evidence showing an actual decrease in herbivores due to the predators (Kromp, 1999). As well, the importance of trees and shrubs in these studies is not consistent. Some studies show these are important in the habitat of predators, while others show that the grass-herbacious layer is by far the most important (Dennis & Fry, 1992). Nicholls *et al*. (2001) however, recently found that a shrubby corridor through a vineyard increased predator densities by providing an alternate food to the variably available field herbivores, and that this did in fact lead to a decrease in herbivore density. As discussed above however, even if trees and shrubs are not important themselves in the habitat of some predators, they may act to preserve the lower grass/herbacious strata that are important. In a simulation study, Topping and Sunderland (1994) found that stable and diverse margins were best for maintaining high populations of predators. Woody vegetation could help to stabilize the field margin habitats by offering protection from some disturbances such as grazing, and increase structural diversity.

Herbivorous insects and fencerows

Examining the effects that woody borders may have on herbivorous insects presents additional challenges because the aims of insect conservation and agriculture may not result in similar recommendations. Conservation requires that woody borders aid in maintaining viable populations of as many native insect species as possible. Agriculture demands that woody borders not lead to increased herbivory in crops, and preferably that they help to limit populations of crop pests. There are many different ways in which woody borders may have an effect on assemblages of herbivorous insects in crop fields.

Field margins may offer complementary habitat (*sensu* Dunning *et al.*, 1992; Morris & Webb, 1987) for some insect species for foraging (Bowden & Dean, 1977; Hawkes, 1973), over-wintering (Dennis & Fry, 1992), summer aestivation (Manglitz, 1958), and mating (Hawkes, 1973). Woody vegetation has been suggested to increase the value of the field margin for the various insect activities in several of these studies. Having complementary habitats in the landscape should lead to an increase in insect diversity because some species in crop fields will require the woody borders to complete some part of their life cycle. In addition to the possible role as complementary habitat, woody borders may function as the sole habitat for some herbivore species. Regardless of the mechanisms involved, the increase in habitat heterogeneity resulting from woody borders should lead to an increase in the diversity of herbivorous insects in the landscape.

If woody borders are complementary habitat for some species and are exempt from disturbances within the adjacent field as mentioned above, they could act as refuges during disturbances such as pesticide application (Dyer & Landis, 1997; Marc *et* al., 1999; Powell, 1986; Reichart & Lockley, 1984), harvesting, and livestock grazing. This could increase density of species that utilize such refugia, and increase richness if some species rely on the woody borders to maintain viable populations.

The effects that woody borders have on herbivore species in crop fields could be largely determined by the effect that they have on the dispersal of these species. Studies have shown that linear barriers (Mader *et al*., 1990), field margins (Jepson, 1994; Thomas *et al.*, 1998), and woody borders in particular (Bowden & Dean, 1977; Frampton *et al.*, 1995; *Lewis*, 1969; Mauremooto *et al.*, 1995) can reduce insect dispersal. This could lead to two main effects on the movement of herbivores. The permeability of patch boundaries can be an important factor in determining emigration from the patch (Stamps *et al.*, 1987). If woody borders act as movement barriers to some herbivore species then some dispersing individuals will remain in the crop field, and a population increase may result because some individuals will turn back into the crop field upon encountering the woody borders at the field edge. Bach (1988) found such an increase in a leaf beetle (Coleoptera: Chrysomelidae) in host plant plots surrounded by non-host vegetation. Some field margins may also make it harder for herbivores to find suitable crop fields (Fry 1994). These effects are not mutually exclusive.

Although a reduction in movement could be a benefit to agriculture if it leads to reduced colonization of fields by herbivores, this must be balanced against a reduction in insect pollination, and a possible loss of diversity if some species are unable to maintain viable regional populations. Because agricultural areas are a dynamic mosaic of patches (Duelli *et al.*, 1990) viable populations must continually repopulate local extinctions as crops in different fields are removed (den Boer, 1981; Duelli *et al.*, 1990; Fahrig and Merriam, 1994; Hanski, 1994).

There are several different effects that woody borders may have on herbivorous insects in agricultural fields, and associated with each is a predicted effect on both the insect richness and density. This makes it very difficult to predict the overall effect of woody borders on insect assemblages. Different agricultural disturbance regimes undoubtedly add an additional element of complexity to this problem. Therefore it is difficult to suggest ways in which to maximize insect conservation while minimizing insect damage to crops. We suggest that the best way to look at the overall effects of woody borders on insect assemblages is through field studies on broad taxonomic groups. Such studies should be informed by studies on individual species, and well-parameterized simulation studies.

Four studies in alfalfa fields

Members of the Landscape Ecology lab at Carleton University have recently carried out four studies on insects in alfalfa fields using intensive sampling of fields within one landscape (Fahrig & Jonsen, 1998), a computer simulation (Bhar & Fahrig, 1998), and focal patch approaches (Jonsen & Fahrig, 1997; Holland & Fahrig, 2000). Focal patch studies consider the effect of predictor variables measured within a landscape (amount of woody border, for example) on the response variable, which is measured within a patch embedded in the larger landscape (Brennan *et al.*, in press). The individual landscape (and corresponding focal patch) are the unit of replication in this type of study (Brennan *et al.*, in press; figure 1).

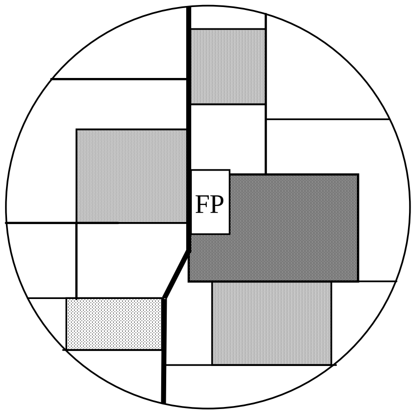

Figure 1 Hypothetical example of a single sampling landscape in a focal patch study. The response variable is measured within the focal patch (FP) and the predictor variables are measured within the landscape.

This section describes the results of the four alfalfa field insect studies and how these results relate to woody borders around the alfalfa fields. Table 1 summarizes the results of these studies. The next section examines what these results reveal about the hypothesized effects of woody borders, and suggests what research is still necessary.

Study 1: Fahrig and Jonsen (1998) looked at the effects of alfalfa patch isolation, age (years in alfalfa), and disturbance regime on insect assemblages in 31 alfalfa fields in a 2km x 4km landscape. Insects were sampled by sweepnet and the above field characteristics were quantified by air photographs, direct observation, and talking to landowners. Fahrig and Jonsen found that patch isolation had a positive effect on overall insect family richness as well as on the family richness within several orders. A lack of a negative effect of isolation on species richness would have implied that many insects are able to easily colonize fields at the distances considered (1-135m). The observed positive effect is likely due to the fact that alfalfa fields with higher isolation are surrounded by other types of crops (Fahrig and Jonsen, 1998). This increased habitat diversity could lead to increased insect diversity.

Fahrig and Jonsen also found that insect richness was maximized with less frequent harvesting, and in fields of intermediate age (2 years in alfalfa; study range: 1-3 years). These results show that the temporal aspects of the crop habitat may be more important than the spatial ones for insect diversity. They also suggest relatively easy ways to maximize insect richness in alfalfa fields. Fahrig and Jonsen found no effect of isolation, field age, or disturbance frequency on the overall density of insects within the alfalfa fields sampled.

Table 1. Results of the alfalfa field studies. Results shown are for all insect groups combined; consult appropriate study for effects on specific insect taxa. The results of Bhar and Fahrig (1998) are listed as "Possibly –" because these effects depend on other factors (see text).

	Herbivore density	Herbivore Richness	Study
Patch isolation	No effect	+	Fahrig & Jonsen, 1998
	No effect	No effect	Jonsen & Fahrig, 1997
Patch age	No effect	+ (age^2: -)	Fahrig & Jonsen, 1998
	No effect	No effect	Jonsen & Fahrig, 1997
	Possibly -		Bhar & Fahrig, 1998
Disturbance frequency	No effect	-	Fahrig & Jonsen, 1998
	No effect (g); + (s)	No effect (g); + (s)	Jonsen & Fahrig, 1997
	Possibly -		Bhar & Fahrig, 1998
Landscape diversity	+ (g); No effect (s)	+ (g); No effect (s)	Jonsen & Fahrig, 1997
Amount of woody border in landscape	No effect	+	Holland & Fahrig, 2000
	Possibly -		

+: positive relationship; -: negative relationship; g: effect on alfalfa generalists; s: effect on alfalfa specialists; blank: not considered in study.

Study 2: In a focal patch study, Jonsen and Fahrig (1997) studied the effects of landscape diversity, amount of alfalfa cover, and field isolation on specialist and generalist insect herbivores in the weevil (Coleoptera: Curculionidae) and leafhopper (Homoptera: Cicadellidae) families found in alfalfa fields. They used sweepnet sampling in 26 focal alfalfa fields, and quantified the aforementioned landscape characteristics in a 1km radius landscape around each field.

Jonsen and Fahrig found that landscapes with increasing landscape diversity (Shannon-Wiener index) had greater generalist richness and abundance. While they did not explicitly include woody borders in their analysis of landscape diversity, the finding is still relevant to the present discussion because woody borders represent a distinct habitat feature in the landscape. More diverse landscapes in the Ottawa region are landscapes with more woody borders. Therefore the results suggest that increased landscape diversity through woody borders will probably also lead to increased generalist herbivore richness and abundance.

Jonsen and Fahrig also found that isolation (measured as proportion of alfalfa cover in the landscape and as distance between alfalfa fields) had no effect on the richness or abundance of specialist herbivores. This suggests that these insects are able to find alfalfa fields relatively easily at distances greater than those considered in this study (480m ± 167 s.d.). They also point out that some insect species make very long distance movements. One leafhopper species, *Empoasca fabae* (Harris), migrates thousands of kilometers to fields in Ontario (Pienkowski & Medler, 1966). The effect that different borders have on species at the end of such migratory movements may be much different than during more common, daily movements.

Study 3: In another focal patch study Holland and Fahrig (2000) used sweepnet sampling to look explicitly at the effects of woody borders in the landscape on primarily herbivorous insect assemblages within 35 alfalfa fields. We quantified the amount of woody border within a 1km radius landscape using air photographs for each focal alfalfa field. We looked at the effect of landscape woody borders on the total insect abundance, family richness, species richness and combined abundance of legume-specialist weevils, and abundance of the alfalfa weevil (*Hypera postica* (Gyllenhal), an alfalfa specialist) over two summers. We found that the amount of woody border in the landscape had no effect on the abundance of all insects, legume-specialist weevils, or the alfalfa weevil. These abundance measures were also not related to the field age (range: 1-12 years), or the interaction term between woody border and field age. We included the interaction term because we had predicted that the effect of the woody borders would depend on the age of the field. In younger fields, we expected the woody borders to slow insect movement into the field. Older fields were expected to show more of an increase in abundance in the presence of woody borders due to the trapping effect, mentioned above. The lack of significance of the age, woody border, and interaction terms again suggests that insects are colonizing the fields much faster than was expected, and that woody borders did not slow this colonization, at least not on a time scale of years. It also shows that having woody borders in the area around the alfalfa field did not lead to an increased abundance of herbivores in the fields. Ninety-five percent of the insects sampled in alfalfa fields in the Ottawa area using these methods are herbivores (Fahrig & Jonsen, 1998).

We also found that the amount of woody border in the landscape was positively related to insect family richness. All insects were collected at the centre of the field, so this increase in richness is in addition to any increase within the woody borders themselves.

Study 4: Finally, Bhar and Fahrig (1998) conducted a simulation study to look at the effects of woody borders on herbivorous insects in alfalfa fields in order to predict under what conditions woody borders should be most beneficial. The simulation used a stochastic, individual-based model of insect movement, survival, and population growth. Runs of the model were done in pairs, with each pair consisting of a run in a landscape with woody borders, and a run in the "same" landscape without woody borders. The effects of woody borders on insect survivorship both in the field and during dispersal (by making other suitable fields less apparent, for example) were altered to see under what conditions woody borders had a positive or negative effect on alfalfa pest insects. Crop rotation was also included in the model by randomly assigning a number of years to each field before it was converted to a non-host crop. When this occurred another alfalfa field was added in a different location, simulating the dynamic nature of an agricultural landscape.

The simulation results showed that woody borders were most effective in reducing populations of pest species in crop fields if a short crop rotation cycle was used and if the borders were effective at reducing emigration. This combination should lead to frequent local extinctions with few individuals escaping to other suitable fields. This model also predicts that the reduction of pest species in fields with woody borders over those fields without similar borders will occur when the probability of successful dispersal by the herbivore is high. In other words, if there is a very high probability of the insects dying before moving to another suitable crop field, the woody borders are not necessary to control pest populations and no difference between fields with and without woody borders will be seen. If insects have a high probability of successfully dispersing to another suitable field however, woody borders may be instrumental in controlling pest populations (Bhar & Fahrig, 1998). Again, this effect is dependent on the woody borders actually reducing movement through them.

Implications of the alfalfa field studies and future research

The results of the three empirical studies on insects in alfalfa fields mentioned above all seem to indicate that the insects studied are able to quickly find the fields. Neither the isolation of the fields, nor the amount of woody border in the landscapes around them seem to slow the insect's search for them, at least on a scale of years. Studies of arthropod movement by Duelli (1988) and Duelli *et al*. (1990) found a very high turnover rate of flying insects in an agricultural area, as well as a fairly high rate of non-flying insect turnover. Duelli *et al*. (1990) concluded that colonization of suitable patches by insects was not limited by dispersal. The results above are in agreement with this conclusion.

However, several studies have shown that hedgerows in particular can, in fact, act as barriers to dispersal out of crop fields (see Herbivorous insects and fencerows). Paradoxically, the fact that insects are able to locate suitable fields relatively quickly means that woody borders may be useful in reducing herbivore populations in agricultural fields. The combined effects of insects finding fields relatively easily and some types of woody borders acting as barriers to dispersal from fields suggests that these borders may be beneficial to agriculture in controlling herbivore species in accordance with Bhar and Fahrig's (1998) model. Their results suggested that the benefits of woody borders are maximized when the insects are very good at finding suitable fields.

Regardless of the effectiveness of woody borders in controlling populations of herbivores in crop fields they have not lead to increases of herbivores. They have however, lead to increased richness. Woody borders are helping to protect biodiversity within agricultural landscapes without causing crop losses. Further studies could help to increase their effectiveness in controlling crop pests to further increase their value.

These studies suggest two questions which need to be addressed in order to further elucidate the effects of woody borders on herbivorous insects: how effective are individual insects at finding suitable crop fields, and how permeable are woody borders to them? These two questions have been difficult to address at large scales because we have had to rely on inferring mechanisms from the assemblages sampled in focal patch type studies (figure 1). This is a problem not only because we can only make best guesses at the mechanisms behind the patterns we find, but also because we must map out the vegetation on a human scale, delineating large parcels of land as suitable or not suitable and assuming any insect found in a new field must have come from one of the other patches we have delineated as suitable. This ignores the heterogeneity of vegetation within these other patches, and the fact that such a coarse classification must ignore many features. Jonsen and Fahrig (1997) state that resources for generalist leafhoppers may be found even in roadside verges. Although the situation may be different for more specialized pest species, even legume specialist weevils can be found in this situation, and on heavily managed lawns (pers. obs.).

Newer technology is being successfully used in fieldwork to look at daily movements of insects. Osborne *et al.* (1999) have used harmonic radar to monitor the movements of bees within a ½ kilometer area from a stationary receiver. It is possible that we may soon be able to do similar studies on even smaller insects. Such studies could have many applications in discovering how pest insects search for crop fields in landscapes, and the effect that different types of woody borders have on this search.

The mechanisms involved in finding host plant fields are probably very different for insects moving from field to field, than for insects at the end of a migration at high altitude. The latter situation probably involves a random landing at some location. It may be interesting for future studies to consider species that overwinter separately from species that migrate to the study area.

There remains much research to be done on the effects of woody borders on insect assemblages in agricultural landscapes. An important next step is to understand how herbivorous insects search for suitable fields within a landscape. It is particularly important to find out how different woody border types interact with this searching behaviour so that the benefits of woody borders to agriculture can be maximized. In the meantime woody borders are protecting biodiversity with no apparent cost to agriculture.

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