Local and broadscale landscape structure differentially impact predation of two potato pests

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Abstract. Agricultural habitats are the recipients of ecosystem services provided by mobile arthropods like pollinators and natural enemies. These organisms can disperse between non-crop habitats and crops and can benefit from resources in non-crop areas. Thus, it may be important to conserve non-crop habitats to maintain ecosystem services within crops. However, even single ecosystem services, such as pollination or predation of pests, may be provided by a complex of species. Different species may respond to landscape structure at differing spatial scales. This raises the question: What scales should conservation take place at to sustain an ecosystem service? Here, we examine variation in predation of two potato pests in response to landscape structure. Specifically, predation of Colorado potato beetle, Leptinotarsa decemlineata, and green peach aphid, Myzus persicae, were quantified in potato and field-margin habitats set in landscapes that varied at different scales. At a local scale (meters), potato fields of different sizes were bordered by different areas of grassy field margin. At a broad scale (kilometers), these habitats were set in landscapes composed of varying percentages of non-crop habitat. Predation of both pests was associated with landscape structure, but this relationship occurred at different scales for each pest and interacted differently with habitat type. Predation of L. decemlineata eggs was greater in field margins than in the potato crop and increased in both habitats when field margins were large relative to potatoes. In contrast, aphid predation in field margins increased with the area of non-crop habitat within 1.5 km, but did not change in adjacent potato. These data emphasize that, even a single ecosystem service, such as predation of pests, can be influenced by landscape structure at multiple scales. More generally, it may be necessary to conserve heterogeneity both at local scales (individual farm fields) and broad scales (entire mosaic landscapes) to maintain ecosystem services. This may be especially true for ecosystem services that are the aggregate result of the actions of many species or ecological processes.

Key words: agricultural environmental schemes; Colorado potato beetle; conservation biological control; ecosystem services; field borders; green peach aphid; landscape context; Leptinotarsa decemlineata; Myzus persicae; predation; spatial scale.

Introduction

Conserving non-crop habitats may enhance ecosystem services that arthropods provide to agriculture. Predatory arthropods can reduce pest populations, and bees are important pollinators of many crops (Losey and Vaughan 2006). Because these organisms are mobile, they can move between multiple crop and non-crop habitats in their lifetime (Wratten et al. 2003, Williams and Kremen 2007). As a result, the availability of resources in surrounding habitats can affect biocontrol and pollination services in crops (Landis et al. 2000, Williams and Kremen 2007). In particular, non-crop habitats may provide alternative foods and shelter that cannot be found in simplified crop monocultures (Bianchi et al. 2006). This raises the possibility that conserving non-crop habitats in farmscapes can increase ecosystem services (Kremen et al. 2004, Bianchi et al. 2006). However, in order to do so effectively, it is necessary to understand the spatial scales at which landscape structure influences their provision (Kremen 2005).

The impact of habitats outside of crops on ecosystem services may vary with spatial scale, suggesting that not all scales of management will be equally effective (Thies and Tscharntke 1999, Tscharntke et al. 2005). Correlations between ecosystem services and landscape structure often peak at specific scales and are weaker at others, a result shown for both parasitism of pests (Thies et al. 2003) and pollination (Kremen et al. 2004). This suggests that there are optimal (and suboptimal) scales of landscape management for service-providing arthropods. In particular, the appropriate scale of management may depend on the mobility of the species providing an ecosystem service (Roland and Taylor 1997). Conserving non-crop habitats immediately adja-
cent to crops may be important when services are provided by species of low mobility (Tscharntke et al. 2007). For example, planting strips of grass every 200 m in wheat fields may enhance predation by ground beetles by providing them a place to overwinter (Collins et al. 2002). Providing habitats immediately adjacent to wheat is important because it limits the distance these beetles (many of which are ground-crawling and may only move a few hundred meters per year) have to disperse to enter crops (Wratten et al. 1998). In contrast, honey bees may travel 0.6–10 km during foraging trips (Steffan-Dewenter and Kuhn 2003), and their abundance in local habitat patches is affected by the structure of the landscape on the scale of kilometers (Steffan-Dewenter et al. 2002). For highly mobile species like honey bees, conserving a mosaic of crop and non-crop habitats at a broad, kilometer scale may enhance the services they provide (Tscharntke et al. 2005).

These results suggest that not all scales of management will be equally effective at conserving a given ecosystem service because each service may be provided by species that experience landscape heterogeneity at a unique spatial scale (Tscharntke et al. 2005, 2007). However, a single ecosystem service is often the aggregate result of the actions of multiple species (Balvanera et al. 2005). For example, solitary bees and honey bees both contribute to pollination, but differ greatly in dispersal ability and respond to landscape structure at different scales (Steffan-Dewenter et al. 2002). Furthermore, there can be multiple targets for ecosystem services in a single crop. For example, most crops are attacked by multiple pest species (Foster and Flood 1995), which could be attacked by natural enemies that use the landscape at different scales. This raises the possibility that non-crop habitats should be conserved at multiple spatial scales to maintain aggregate function.

The relative impact of local and broadscale landscape structure on predation of pests is hard to evaluate. Most field studies have examined the impact of non-crop areas on predation across local (Landis et al. 2000) or broad scales (Bianchi et al. 2006), but not both (but see Thies and Tscharntke [1999]). Furthermore, most studies have only quantified predation of single pest species (Bianchi et al. 2006). To build on these studies, we simultaneously examined the impact of local and broadscale landscape structure on predation of two insect pests of potatoes in Wisconsin, USA: the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), and green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). At a local scale, the influence of grassy field margins on predation was quantified, while at a broad scale, predation of pests was correlated to the composition of the landscape within 1.5 km of fields (Fig. 1). We then asked: (1) is there evidence that non-crop habitats enhance predation of these pests, (2) what is the relative evidence for local and broadscale impacts of non-crop habitats on predation of each pest, and (3) does landscape structure impact predation of these two pests at the same, or different spatial scales?

**Methods**

**Study organisms**

To answer these questions, we related predation of Colorado potato beetle (CPB) eggs and green peach aphids (GPA) to local and broadscale landscape structure. Both are important pests of potato in Wisconsin (Mahr et al. 1995). CPB larvae and adults feed on potato foliage, with one to two generations occurring each year (Mahr et al. 1995). Adults emerge in late May and lay clusters of 20–60 eggs on the underside of leaves (Hare 1990); these hatch into larvae that develop into adults of the first generation. GPA is a sap-sucking insect and is important as a vector of potato viruses (Mahr et al. 1995). It reproduces continually by parthenogenesis, with populations typically peaking in August (Mahr et al. 1995). These two pests are attacked by a diverse assemblage of arthropod predators that vary in life history and dispersal ability (van Emden et al. 1969, Hough-Goldstein et al. 1993). During this study a variety of predators were observed eating CPB egg masses, including lacewing larvae (Neuroptera: Chrysopidae), minute pirate bugs (*Orius* spp., Hemiptera: Anthocoridae), harvestmen (Opiliones), coccinellids (primarily *Coleomegilla maculata*), katydids (Orthoptera: Tettigoniidae), and mirids (Hemiptera) (P. Werling, unpublished data). Similarly, a variety of predators were found on aphid-infested plants: hoverfly (Diptera: Syrphidae) and lacewing larvae were observed attacking aphids, and *Orius* spp. and spiders (Araneae) were observed foraging on infested plants. Thus, predation of these pests could change with landscape structure at a variety of scales depending on which of these varied taxa are functionally important.

**Study landscape and site selection**

Study sites were in central Wisconsin in Adams, Marquette, Portage, and Waushara counties. All sites were in commercial potato fields of farmers in the Wisconsin Healthy Grown program. To sell under the Healthy Grown brand name, farmers adhere to integrated pest management and ecosystem standards (Benbrook et al. 2002, Sxesson 2006). Participants use narrow-spectrum (i.e., low nontarget toxicity) insecticides and conserve grassland, savanna, and wetland habitat on their farms (Sxesson 2006).

The composition of the landscape surrounding Wisconsin potato farms varies at local and broad spatial scales. At a local scale, potato fields are bordered by uncultivated, grassy field margins (Fig. 1A). Field margins are located along the edges and corners of potato fields and are dominated by perennial grasses and associated forbs (percent cover of grass: $\bar{X} = 75\%$, $SE = 3$, $n = 95$, 1-m quadrats; Appendix A). Most vegetation has regenerated naturally, although 22% of field margin...
area (137 ha out of 632 ha) had been planted to forages (primarily grasses or mixtures of grasses and legumes) or mowed for hay during the study (land cover percent estimated with a geographic information system [GIS]). At this local scale, potato fields vary in area and are surrounded by different areas of field margin (Fig. 1B).

At a broader scale, potato fields and grassy margins are set in landscapes composed of varying percentages of non-crop habitats (Fig. 1C). To capture this variation, fields were randomly chosen from five strata defined by broadscale landscape composition: fields were set in 1.5-km landscapes composed of (1) 0–20% non-crop, (2) 21–40%, (3) 41–60%, (4) 61–80%, and (5) 81–100% non-crop habitat. New fields were chosen each year (CPB, n = 19 fields in 2005, n = 22 in 2006; GPA, n = 16 in 2005, n = 16 in 2006). Given that some fields were used for both CPB and GPA experiments, there were n = 50 unique fields used in this study. Not all growers that participated in the CPB experiment were comfortable participating in the GPA experiment given concerns about aphid infestations. Therefore, a subset of fields used in the CPB experiment were supplemented with additional fields for the GPA study (2005, 10 fields were used for both the CPB and GPA experiment supplemented with 6 fields for GPA; 2006, 13 fields used for CPB and GPA, supplemented with 3 fields for GPA). Inter-field distances ranged from 1.3 to 100 km, with all but 10 of 1225 possible pairs of fields >3 km apart. These fields were also set in landscapes that varied at local scales: potato fields were 7–81 ha in size and were surrounded by 2–27 ha of field margin. Furthermore, local and broadscale landscape structure were not correlated (Spearman’s ρ = 0.18, P = 0.22), allowing us to independently assess the effects of both on predation.

Measuring predation: CPB.—Predation of CPB eggs was quantified in potatoes and adjacent grassy margins at each field in June 2005 and 2006. Methods varied slightly between years as procedures were improved to reduce experimental error (Appendix B). Egg masses were collected from laboratory colonies and field plots, and the number of eggs per mass were counted before exposure in the field (X = 36 eggs/mass, SE = 0.4). In 2005, 12 egg masses were placed in the grassy field margin and in the adjacent potato crop at each field site, with egg masses in potatoes evenly distributed (i.e., 3 egg masses/location) between crop edges and centers (Appendix B). An additional three egg masses were deployed in field margins and potatoes and covered with 23 × 46 cm mesh cages to exclude predators (total of 30 egg masses/site; Appendix B). Importantly, we found no evidence that these cages directly affected egg mortality (Appendix C). Thus, they provided an accurate estimate.
of egg mortality in the absence of predation. In 2006, eight uncaged and four caged egg masses were placed in field margins and in the edge and center of adjacent potatoes (total of 36 egg masses/field; Appendix B). In 2005, CPB egg masses were collected on potato leaflets that were transported to the field and carefully attached to existing vegetation (1 egg mass/plant), while in 2006 potted plants were infested with a single egg mass in the laboratory and brought to the field (Appendix B). Eggs were placed in 10 fields the week of 13 June 2005 and 9 fields the following week and collected within 2–3 days (at two sites, eggs were collected after 4 and 5 days). In 2006, eggs were deployed at 8 fields on 3 June, 8 fields on 9 June, and 6 fields on 15 June and collected after two days. Eggs were returned to the laboratory and placed in a 23°C growth chamber to quantify the proportion of each egg mass that hatched. The geometric mean of hatch rates was used to calculate daily survival rates, \( S \), with daily mortality calculated as \( 1 - S \) (van der Toorn 1997). Hatch rates were used to estimate mortality because predation does not always leave visible damage (Koss 2003). Predation was quantified by subtracting off background mortality estimated from egg masses in predator-exclusion cages (Chang and Snyder 2004). The average proportion of eggs predated per day, \( \text{EGG}_{ij} \), was quantified for the \( i \)th site and \( j \)th habitat as

\[
\text{EGG}_{ij} = \frac{\sum_k \text{EM}_{u,ijk}}{n_{a,ij}} - \frac{\sum_k \text{EM}_{c,ijk}}{n_{c,ij}}
\]

where \( \text{EM}_{u,ijk} \) is the per day rate of egg mortality for the \( k \)th egg mass placed in the \( j \)th habitat at the \( i \)th site that was uncaged, \( \text{EM}_{c,ijk} \) is the comparable rate for eggs protected from predation by cages, \( n_{a,ij} \) and \( n_{c,ij} \) are the number of uncaged and caged egg masses in each location, and there are \( i = 41 \) fields and \( j = 2 \) habitats per field (field margin or potato). Egg predation never differed between potato field edges and centers (i.e., within sites, predation did not differ with distance away from field margins), and there was little evidence that this changed with landscape structure (i.e., changes in predation with landscape structure were similar near and far from field margins; Appendix D). Thus, a pooled estimate of predation in potatoes was used in analyses.

**Measuring predation: GPA.**—Predation of GPA was measured in 16 fields in 2005 and 2006. Aphids were maintained in colonies started by collecting aphids from local greenhouses (Dane County, Wisconsin). In 2005, one-month-old Chinese cabbages (Brassica rapa ssp. pekinensis var. ‘Michihili’) potted in 10 cm square pots were infested with 20 aphids each. Five plants spaced 5 m apart were placed in a haphazardly selected length of field margin and five more in adjacent potatoes (30 m from the field margin). One plant in each habitat was covered with a mesh cage to exclude predators. We found little evidence these cages affected GPA population growth in the absence of predators (Appendix C). In 2006, one-month-old potato plants were infested with 25–30 aphids (plants as for CPB; Appendix B); five caged and uncaged plants spaced 5 m apart were placed in the field margin and 30 m away in potato at each site. Initial aphid numbers were recounted upon deployment at field sites. In 2005, plants were placed in 8 fields on 13 August and 8 more fields on 20 August. In 2006, plants were deployed in 7 fields on 4 August, 6 fields on 11 August, and 3 fields on 18 August. Plants were collected after two days in 2005 and three days in 2006 and the number of aphids per plant were counted. The ratio of the final number of aphids to initial numbers was used as a measure of aphid population change. Suppression of aphid population growth by predators was then quantified using log ratios (LR):

\[
\text{LR}_{ij} = \log_{10} \left( \frac{\sum_k A_{u,ijk}}{n_{a,ij}} + \frac{\sum_k A_{c,ijk}}{n_{c,ijk}} \right)
\]

where \( \text{LR}_{ij} \) calculated for the \( i \)th site and \( j \)th habitat becomes increasingly negative as predators suppress aphid population growth, \( A_{u,ijk} \) and \( A_{c,ijk} \) are the ratios of final to initial aphid numbers on the \( k \)th uncaged and caged plant and \( n_{u,ijk} \) and \( n_{c,ijk} \) are the number of uncaged and caged plants at each site and habitat. Note that in 2005 estimates of aphid growth on caged plants were averaged across habitats for each site, as there was only one caged plant per habitat (this reduced the impact of cages with extremely high or low aphid growth on LR estimates).

**Quantifying variation in landscapes**

Local and broadscale landscape structure was quantified using ArcGIS 9 (ESRI 2005). At a local scale, the ratio of field margin to potato area, \( L_f \), was measured (Fig. 1B). To quantify \( L_f \), 2005 air photos of 1-m resolution were used in combination with on-site determination of cover type to calculate the area of each potato field and all field margin habitat within 200 m of the crop edge (USDA 2005). These photos were used for 2005 and 2006 because landscapes around study fields changed little between years. Tree lines <20 m in width and >50 m from contiguous forest were also categorized as field margin because thin tree lines had grassy understories and/or were bordered by strips of grass. A distance of 200 m was chosen because this was the width of the largest field margin and because it represents the distance that some ground-dispersing predators travel in a season (Baars 1980, Thomas et al. 1991). This metric was positively correlated with increases in field margin area and field perimeter to area ratio and negatively with potato area (Table 1). Thus, as \( L_f \) increased, potato fields became smaller and their perimeter to area ratio increased, resulting in any given area of the crop being closer to large areas of field margin (Fig. 1B).

At a broad scale, the percentage of the landscape within 1.5 km of field centers composed of non-crop
habitat, $B$, was quantified using the 2001 National Landcover Dataset (Fig. 1; Homer et al. 2004). Calculations of $B$ based on these data were highly correlated with $B$ calculated from 2005 data that were available for a subset of sites (Spearman’s $\rho = 0.92$, $P < 0.0001$, $n = 15$), suggesting the 2001 National Landcover Dataset provided information about contemporary landscapes. As $B$ increased, landscapes changed from being dominated by agriculture to include forests, grasslands, scrub, and wetlands (Table 1). A 1.5-km scale was chosen because other studies have found that natural enemy abundance and diversity are correlated to non-crop area over this distance (Thies and Tscharntke 1999, Werling and Gratton 2008). Furthermore, percentage non-crop at this scale is correlated with percentage non-crop at smaller (correlation with percentage non-crop within 0.5 km: Spearman’s $\rho = 0.68$, $P < 0.0001$) and broader scales (correlation with percentage non-crop within 3 km: Spearman’s $\rho = 0.84$, $P < 0.0001$), indicating this metric contained general information about broadscale changes in landscape structure.

**Data analysis**

We used multiple models to compare evidence for local and broadscale effects of non-crop habitats on predation. Three questions were tested. (1) Overall, is there evidence that predation is nonrandomly associated with the amount of non-crop habitats in landscapes? (2) If so, at what scales do non-crop habitats influence predation of CPB and GPA? (3) Are these scales the same or different for predation of these two pests? To accomplish this, predation data were related to models containing different combinations of local and broadscale landscape variables, each representing a unique hypothesis about the impact of landscape on predation (Table 2). At a local scale, predation was measured in two habitat types ($L_h$), field margin and potato. If natural enemies aggregate to resources in field margins, predation could be increased in field margins compared to potatoes (Collins et al. 2002, Tylianakis et al. 2004). If these natural enemies also enter the crop, we expected that predation would increase with $L_f$. This was expected because, as potato fields get smaller and field margins larger, any given area of the crop will be closer to large areas of resource-rich habitat (Fig. 1B). Furthermore, $L_f$ and $L_h$ could interact: this could occur if key predators use resources in field margins but do not enter crops at high rates (Duelli et al. 1990, Werling and Gratton 2008). In contrast, if natural enemies are highly dispersive, we expected predation to increase with $B$ (Gardiner et al. 2009). However, there could again be an interaction if predators are “non-crop” specialists that disperse freely among non-crop habitats but do not enter potato ($L_h \times B$). Finally, local and broadscale landscape structure could simultaneously influence predation (Thies and Tscharntke 1999). This could occur if the benefits of conserving local non-crop habitats depend on broadscale landscape structure ($L_f \times B$), or if multiple predators of different dispersal abilities attack a single pest (models with main effects of both $L_f$ and $B$).

Model fit statistics were calculated for each model by conducting separate analyses for predation of each pest in SAS PROC MIXED (SAS Institute 2002). Data were

**Table 1.** The two landscape variables used in analysis of predation of eggs of the Colorado potato beetle (*Leptinotarsa decemlineata*) and green peach aphids (*Myzus persicae*) were correlated with a variety of changes in local and broadscale landscape structure in central Wisconsin, USA.

<table>
<thead>
<tr>
<th>Landscape attribute</th>
<th>Median</th>
<th>Range</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potatoes (ha)</td>
<td>27</td>
<td>7–81</td>
<td>−0.48**</td>
</tr>
<tr>
<td>Perimeter to area</td>
<td>79</td>
<td>43–203</td>
<td>0.42**</td>
</tr>
<tr>
<td>Field margin (ha)</td>
<td>11</td>
<td>2–27</td>
<td>0.53**</td>
</tr>
</tbody>
</table>

Notes: At a local scale, the ratio of field margin to potato area ($L_f$) was correlated with decreases in potato field area and increases in the perimeter-to-area ratio of fields and the area of field margin within 200 m of the crop. At a broad scale, the percentage area of non-crop habitats within 1.5 km of potatoes was measured ($B$); a variety of non-crop habitats increased in area as this measure increased, while the area of cropland declined. Correlations are Spearman’s rank correlation coefficient ($\rho$). Medians and ranges are given for each descriptor of landscape structure.

**Correlation of local landscape attributes with $L_f$**

<table>
<thead>
<tr>
<th>Landscape attribute</th>
<th>Median</th>
<th>Range</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest (%)</td>
<td>24</td>
<td>2–65</td>
<td>0.88**</td>
</tr>
<tr>
<td>Grassland (%)</td>
<td>2</td>
<td>0–10</td>
<td>0.46**</td>
</tr>
<tr>
<td>Scrubland (%)</td>
<td>0</td>
<td>0–5</td>
<td>0.44**</td>
</tr>
<tr>
<td>Herbaceous wetland (%)</td>
<td>0</td>
<td>0–14</td>
<td>0.39**</td>
</tr>
<tr>
<td>Pasture (%)</td>
<td>9</td>
<td>0–31</td>
<td>0.008</td>
</tr>
<tr>
<td>Open space (%)</td>
<td>4</td>
<td>2–9</td>
<td>−0.12</td>
</tr>
<tr>
<td>Barren (%)</td>
<td>0</td>
<td>0–2</td>
<td>−0.24</td>
</tr>
<tr>
<td>Urban (%)</td>
<td>1</td>
<td>0–9</td>
<td>−0.42**</td>
</tr>
<tr>
<td>Cropland (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
</tbody>
</table>

Notes: At a local scale, the ratio of field margin to potato area ($L_f$) was correlated with decreases in potato field area and increases in the perimeter-to-area ratio of fields and the area of field margin within 200 m of the crop. At a broad scale, the percentage area of non-crop habitats within 1.5 km of potatoes was measured ($B$); a variety of non-crop habitats increased in area as this measure increased, while the area of cropland declined. Correlations are Spearman’s rank correlation coefficient ($\rho$). Medians and ranges are given for each descriptor of landscape structure.

**Correlation of land cover with $B$**

<table>
<thead>
<tr>
<th>Landscape attribute</th>
<th>Median</th>
<th>Range</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
<tr>
<td>Grassland (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
<tr>
<td>Scrubland (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
<tr>
<td>Herbaceous wetland</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
<tr>
<td>Pasture (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
<tr>
<td>Open space (%)</td>
<td>52</td>
<td>17–82</td>
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</tr>
<tr>
<td>Barren (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
<tr>
<td>Urban (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
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<td>Cropland (%)</td>
<td>52</td>
<td>17–82</td>
<td>−0.99**</td>
</tr>
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Table 2. Summary of model selection statistics for $i = 18$ models predicting predation of eggs of the Colorado potato beetle (CPB, *Leptinotarsa decemlineata*) and green peach aphids (GPA, *Myzus persicae*) as a function of different combinations of local ($L$) and broadscale ($B$) landscape variables.

<table>
<thead>
<tr>
<th>$i$</th>
<th>Predictor variables $K_i$</th>
<th>$-2\log(L)$</th>
<th>$AIC_c$</th>
<th>$w_i$</th>
<th>$\Delta_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>None</td>
<td>5</td>
<td>CPB</td>
<td>GPA</td>
<td>0.0037</td>
</tr>
<tr>
<td>2</td>
<td>$L_h$</td>
<td>6</td>
<td>CPB</td>
<td>GPA</td>
<td>0.0099</td>
</tr>
<tr>
<td>3</td>
<td>$L_f$</td>
<td>6</td>
<td>CPB</td>
<td>GPA</td>
<td>0.0144</td>
</tr>
<tr>
<td>4</td>
<td>$L_h, L_f$ (CPB best model)</td>
<td>7</td>
<td>CPB</td>
<td>GPA</td>
<td>0.0012</td>
</tr>
<tr>
<td>5</td>
<td>$L_h, L_h, L_h, L_f$</td>
<td>8</td>
<td>CPB</td>
<td>GPA</td>
<td>0.13</td>
</tr>
<tr>
<td>6</td>
<td>$B$</td>
<td>6</td>
<td>CPB</td>
<td>GPA</td>
<td>0.00012</td>
</tr>
<tr>
<td>7</td>
<td>$L_f, B$</td>
<td>7</td>
<td>CPB</td>
<td>GPA</td>
<td>0.0032</td>
</tr>
<tr>
<td>8</td>
<td>$L_h, B, L_h \times B$ (GPA best model)</td>
<td>8</td>
<td>CPB</td>
<td>GPA</td>
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Notes: Local-scale variables are the type of habitat in which predation was measured ($L_h =$ field margin or potato) and the ratio of field margin area to potato area ($L_f$), while the percentage of the landscape within 1.5 km of fields composed of non-crop habitats was measured at the broad scale ($B$). Models with substantial support ($\Delta_i \leq 2$) are highlighted in bold. Data suggest that different models best explain predation of CPB (model 4) and GPA (model 8).

Results

Predation of CPB eggs

Data suggest that non-crop habitats impacted CPB predation at local, but not broad, spatial scales. Overall, there was strong evidence that including landscape variables improved prediction over the null model (likelihood-ratio test for global landscape model: $\chi^2 = 30.4$, df = 7, $P < 0.001$). Two models were substantially supported by the data (Table 2). However the second best model (the global model) contained six fixed effects (Table 2). In contrast, the AIC-best model contained only two fixed effects: it predicted egg predation as a function of habitat type ($L_h$) and the ratio of field margin area to potato area, $L_f$ (Table 2). Consequently, this simpler model was used for inference. In support of this model, the average proportion of eggs predated per day was greater in field margin habitats ($\bar{X} = 0.09$, SE = 0.02) compared to potatoes ($\bar{X} = 0.02$, SE = 0.008). In both habitats, predation increased as the ratio of field...
margin to potato area increased (Fig. 2A, B). In fact, the best model predicted that average predation in potatoes increased from causing 0% egg mortality per day to 11% over the observed range of $L_f$ (Fig. 2B). In contrast, CPB predation changed little with the percentage of non-crop habitat within 1.5 km of fields. Regression lines were fitted using the AICc best model (Table 2). Predation is shown for each field as the average proportion of eggs killed per day in uncaged egg masses minus mortality of eggs in predator-exclusion cages (see Materials and methods: Eq. 1). Negative values occurred when predation was low, resulting in cage mortality occasionally exceeding mortality of uncaged eggs. Note that y-axis scales in panels (A) and (C) differ from those in panels (B) and (D).

**Predation of GPA**

The presence of non-crop habitats was associated with changes in aphid suppression (likelihood-ratio test: $\chi^2 = 16.5$, df = 7, $P = 0.02$). However, in contrast to CPB, predation of aphids was not associated with changes in field margin area (Fig. 3A, B). Instead, the two best models predicted GPA predation as a function of the amount of non-crop habitat within 1.5 km of fields (Table 2). The AIC-best model included an interaction between $L_h$ and $B$, suggesting the impact of broadscale landscape composition varied between habitats (Table 2). Specifically, this model predicted that aphid suppression in field margins increased with the percentage of non-crop habitats within 1.5 km of fields (Fig. 3C), while it changed little in adjacent potatoes (Fig. 3D). In field margins, there was a threefold increase in average suppression of aphid growth by predators as non-crop habitats increased from 17% ($LR = -0.3$) to 81% of the landscape ($LR = -0.89$; Fig. 2C). In potato, GPA suppression changed little over the range of $B$ (Fig. 2D).
The second-best model also contained an effect of broadscale landscape composition, but did not include its interaction with habitat type (Table 2). Across all models, Akaike weights suggest that the amount of non-crop habitat at broad scales is the most important predictor of aphid suppression ($w_B = 0.92$), that habitat type is also an important predictor, ($w_{Lh} = 0.73$), but that field margin area is less predictive ($w_{Lf} = 0.35$).

**DISCUSSION**

Do non-crop habitats impact predation of potato pests and at what scales?

Ecosystem services provided by mobile organisms may be influenced by landscape structure at organism-specific scales. This study found that non-crop habitats have a significant impact on predation of both CPB and GPA, but at different spatial scales. Patterns of CPB predation suggest that field margins within meters of the crop influence predation of this pest but that predation is less affected by the amount of non-crop habitat within kilometers (Fig. 2). In contrast, predation of GPA increased with the amount of non-crop habitat within kilometers of fields but was less affected by field margin area (Fig. 3). Furthermore, data suggest that the relationship between predation and landscape structure varied between habitats for GPA (Fig. 2C, D), but not for CPB (Fig. 1A, B). These results concur with an increasing body of research showing that predation and parasitism of pests can be stronger in landscapes with non-crop habitats (Bianchi et al. 2006). However, they
suggest that predation of different pests can be affected by landscape structure at very different scales. Thus, there may be no “one size fits all” scale of management that will conserve predators of every pest. Instead, land conservation may have to be tailored to the scales important for particular pairs of predators and prey (Tscharntke et al. 2007).

Potential mechanisms

Why did non-crop habitats impact predation of these two pests at different scales? Two mechanisms could explain the differential impact of local and broadscale landscape structure on predation of these pests. First, natural enemies with different dispersal abilities may attack each pest. Alternatively, the same predators may attack both pests but respond to landscape structure differently in June (when CPB egg populations peak) and August (when GPA is present). The latter could occur if natural enemies from distant sources are able to disperse into local habitats by the end of the season (Thomas et al. 1991). While this is possible, the first hypothesis is supported by other data. In a companion study, planting native grasses around potato plots increased predation of CPB eggs by enhancing harvestman (Opiliones) abundance (B. P. Werling, J. Harmon, C. Straub, and C. Gratton, unpublished manuscript). Harvestmen disperse via walking (Pinto-da-Rocha et al. 2007); thus, local habitats may increase the effectiveness of ground-crawling predators of CPB such as harvestmen. In contrast, a recent study of aphid predation in soybean (that included sites in Wisconsin) found that both aphid predators and aphid predation responded to landscape structure at a broad scale (Gardiner et al. 2009). These and other studies suggest that aphid predators respond to landscape structure at broad scales (Elliott et al. 2002, Prasifka et al. 2004). Thus, green peach aphid may be attacked by natural enemies that move across the landscape at broader scales than those that attack CPB eggs, and conserving non-crop habitats at kilometer scales may affect aphid predation in local habitats.

How might non-crop habitats have influenced predation of these two pests? Patterns of CPB predation were consistent with the hypothesis that its natural enemies move between field margins and potatoes, and benefit from resources in field margins. Specifically, when one habitat provides resources to predators in another habitat: (1) predators are often more abundant and have greater impacts next to the resource-providing habitat, (2) predation increases with the area of resource-rich habitats, and (3) predation increases in the resource-poor habitat as patches decrease in size (Polis et al. 1997, Wratten et al. 1998, Landis et al. 2000, Collins et al. 2002, Tylianakis et al. 2004). Predation can be greater in resource-rich habitats when predator populations aggregate in these areas (Bianchi and Wackers 2008). Consistent with this prediction, predation of CPB eggs was greater in field margins than potatoes (Fig. 2). Adding resource-rich habitats to landscapes can enhance predator fitness and predation in adjacent crops (Landis et al. 2000, Tylianakis et al. 2004). In addition, the flux of predators between crop and non-crop areas will increase when crop fields are small relative to non-crop habitats (Wratten et al. 1998). In these situations, small field sizes reduce the distance predators have to travel between non-crop and crop habitats, increasing the ability of organisms to access resources in non-crop habitats. Consistent with this idea, we found that predation of CPB eggs increased as field margins became larger and potato fields decreased in size (Fig. 2B, Table 1) suggesting that crop field geometry \((L_f)\) affects organisms that prey on CPB.

Patterns of GPA predation suggest that predators of this pest move between non-crop habitats at the scale of kilometers. Predation of GPA increased in field margin habitats as the area of non-crop habitat in the surrounding 1.5 km increased (Fig. 3C), yet this effect was not observed in potatoes only meters distant (Fig. 3D). One explanation for this pattern is that predators benefit from resources in non-crop habitats but do not enter potatoes, perhaps because it is an unsuitable habitat. In support of this, a previous study found that the abundance of a variety of aphidophagous predators was greater in sweep net samples taken from field margins compared to potato (Werling 2009). Hoverflies, damsel bugs (Hemiptera: Nabidae), lacewing adults, and the coccinellid *Hippodamia parenthesis* were all more abundant in field margins (Werling 2009). This suggests that potato may not be as suitable as field margin for some aphidophagous predators, and could explain why aphid predation increased with non-crop area in field margins but not potato (Fig. 3C, D). Other crops like soybean may be more suitable for aphidophagous predators. Specifically, aphids are generally much more abundant in soybean than in commercial potato fields (B. P. Werling, personal observation), and this may increase predator immigration and reproduction in soybean relative to potato (Evans 2003). This may explain why Gardiner et al. (2009) found positive correlations between the abundance of aphid predators and the area of non-crop habitat in the landscape.

Conserving non-crop habitats to maintain ecosystem services

This study adds to a growing body of knowledge showing that conserving non-crop habitats may be important to maintain the ecosystem services that farmland organisms provide (Bianchi et al. 2006, Ricketts et al. 2008). This study suggests that reducing field margin area and expanding potato fields could alter predation of CPB eggs in potatoes (Fig. 2B). For example, predation could kill 25% to 40% of eggs when field margin and potato habitats are equal in area \((L_f = 1)\); prediction based on extrapolation of 7% daily predation rate for potato over the 4–7 day development of an egg mass). In contrast, mean predation was
essentially zero when field margins were only 12% of the size of adjacent potato fields (Fig. 2B, $L_e = 0.12$). Thus, expanding crop fields and reducing field margin area could substantially alter predation rates of this pest in potato fields. Consequently, conserving these habitats may be essential if predation by natural enemies is to play a role in the management of this pest.

In addition, this study demonstrates that predation of different pests can be impacted by landscape structure at very different spatial scales: CPB predation was increased by the presence of field margins adjacent to crops, while GPA suppression was related to the amount of non-crop habitat within kilometers (Figs. 2 and 3). Given that most crops are attacked by multiple pest species (e.g., Foster and Flood 1995), this suggests that non-crop habitats should be conserved at multiple scales to sustain predation of pests. Specifically, it may be necessary to conserve non-crop habitats at both local (around individual farm fields) and broad scales (across entire mosaic landscapes) if pests are attacked by predators that respond to landscape structure at different scales.

More generally, ecosystem services may be impacted by landscapes at multiple scales when they depend on the activities of multiple species or are the combined result of multiple processes. Consistent differences have been observed between species in the spatial scales at which they respond to landscape structure (Roland and Taylor 1997, Steffan-Dewenter et al. 2002, Schmidt et al. 2008). Consequently, a reasonable hypothesis is that ecosystem services provided by multiple species may frequently require conservation of habitats at multiple scales. In contrast, if ecosystem services are provided by one or a few functionally dominant species (Balvanera et al. 2005, Straub and Snyder 2006), it may be possible to conserve habitat for those species at the single, most relevant spatial scale. Even more generally, ecosystem services that are defined as a composite of multiple ecosystem processes may be more likely to require multiple scales of management. For example, if farmers only valued predation of CPB, then conserving field margins around individual fields could enhance this service (Fig. 2B). Alternatively, if farmers valued control of both CPB and GPA (assuming predation of aphids in field margins was valuable), then this study suggests that local and broadscale conservation of non-crop habitats should be combined (Figs. 2 and 3). Accordingly, the need for multiple vs. single scales of management may depend on how broadly humans define a given ecosystem service.

**Conclusions**

This study provides evidence that predation of different pests is influenced by landscape structure at different spatial scales. Specifically, predation of CPB was affected by the amount of field margin in local landscapes, while predation of aphids was affected by landscape structure at a broad scale. These results demonstrate that conserving non-crop habitats may be important to maintain predation of pests. However, the scale at which non-crop habitats influence predation may vary between pest species. More generally, ecosystem services may require management at multiple spatial scales when these services are the combined result of the actions of multiple species or ecological processes. As agricultural land use changes in response to human demands for food, energy, or recreation, ecosystem services provided by mobile organisms may also be affected. Understanding the spatial scales that influence these services will help raise awareness of the consequences of land-use decisions made at scales ranging from individual farm fields to entire mosaic landscapes. Ultimately, this could enable ecosystem services to become an explicit part of the decision-making process of farmers and policy makers.

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**Literature Cited**


ESRI. 2005. ArcGIS. ESRI, Redlands, California, USA.


APPENDIX A
Plant species and families found in field margins bordering 19 commercial potato fields in 2005 (Ecological Archives A020-038-A1).

APPENDIX B
Procedures for measuring Leptinotarsa decemlineata (CPB) egg predation in commercial potato fields and their grassy field margins in Wisconsin in 2005 and 2006 (Ecological Archives A020-038-A2).

APPENDIX C
Effect of mesh cages on change in numbers of Leptinotarsa decemlineata (CPB) eggs and Myzus persicae (GPA) (Ecological Archives A020-038-A3).

APPENDIX D
Investigating differences in predation of Leptinotarsa decemlineata (CPB) egg predation between potato field edges and centers (Ecological Archives A020-038-A4).

APPENDIX E
Steps taken to select the variance structure and appropriate fixed effects for models relating predation of Leptinotarsa decemlineata (CPB) eggs and Myzus persicae (GPA) to landscape structure (Ecological Archives A020-038-A5).

APPENDIX F
Residual variance estimates ($\sigma^2$) for mixed models predicting predation of green peach aphid, Myzus persicae (GPA), and Colorado potato beetle, Leptinotarsa decemlineata (CPB), eggs (Ecological Archives A020-038-A6).

APPENDIX G
Estimates of effect ($\beta$) of habitat type ($L_h$), ratio of field margin to potato area ($L_f$), percentage non-crop habitat within 1.5 km ($B$), and the interaction of $L_h$ with $B$ on predation of Leptinotarsa decemlineata (CPB) eggs and Myzus persicae (GPA) based on best-fitting models (Ecological Archives A020-038-A7).