



Biocontrol potential varies with changes in biofuel–crop plant communities and landscape perenniality

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Abstract

We examined the potential local- and landscape-level impacts of different biofuel production systems on biocontrol, an important service provided by arthropod natural enemies. Specifically, we sampled natural enemies with sweep nets and measured predation of sentinel pest eggs in stands of corn, switchgrass and mixed prairie in Michigan and Wisconsin (total $n = 40$ for natural enemy sampling, $n = 60$ for egg predation), relating them to crop type, forb cover and diversity, and the composition and heterogeneity of the surrounding landscape. Grasslands with intermediate levels of forb cover and flower diversity supported two-orders of magnitude more natural enemy biomass, fourfold more natural enemy families, and threefold greater rates of egg predation than corn. Data suggest this was in part due to a general increase in biomass, richness and predation in perennial grasslands compared with corn, combined with a positive effect of intermediate levels of forb cover and flower diversity. Specifically, natural enemy biomass and family richness showed hump-shaped relationships to forb cover that peaked in sites with 5–25% forbs, while egg predation increased with floral diversity. At the landscape scale, both natural-enemy biomass and egg predation increased with the area of forest in the landscape, and egg predation almost doubled as the area of herbaceous, perennial habitats within 1.5 km of study sites increased. Our results suggest that floristically diverse, perennial grasslands support diverse and abundant predator communities that contribute to natural pest suppression. In addition, large-scale production of biofuel crops could positively or negatively affect biocontrol services in agricultural landscapes through associated changes in the area of perennial habitats. Biofuel landscapes that incorporate perennial grasslands could support a variety of beneficial organisms and ecosystem services in addition to producing biomass.

Keywords: biodiversity, biofuels, biological control, ecosystem services, land use change

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Introduction

The future sustainability of bioenergy production will depend on our ability to anticipate the impact of different production systems on ecosystem services (Robertson *et al.*, 2008). Biofuel production is slated to expand to meet governmental and societal demands for alternative transportation fuels (Sissine, 2007; European Parliament, 2009). The impact of this expansion on

ecosystem services will depend on the types of biomass crops that are produced (Robertson *et al.*, 2008; Fargione *et al.*, 2009). On the one hand, existing technologies could be used to produce ethanol from corn grown in intensive, annual monocultures (Renewable Fuel Association, 2010). On the other hand, fuels could be derived from 'low-input' perennial grasslands, which could be grown in monoculture or polyculture (Sanderson & Adler, 2008). Existing ecological knowledge suggests that annual and perennial habitats support very different communities (Steenwerth *et al.*, 2002; Van Buskirk & Willi, 2004; Herkert, 2009; Glover *et al.*, 2010) and

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different rates of ecosystem processes (Robertson *et al.*, 2000; Grandy & Robertson, 2007), and that plant diversity can affect primary production and consumer abundance and diversity (Hooper *et al.*, 2005; Haddad *et al.*, 2009). Consequently, the effect of biofuel production on ecosystem services will depend on the types of biomass crops used to support expanding bioenergy production.

Pest suppression is an important ecosystem service that could be affected by biofuel–crop choice at local and landscape scales (Gardiner *et al.*, 2010; Landis & Werling, 2010). Arthropod predators and parasitoids (hereafter ‘natural enemies’) suppress populations of herbivorous crop pests, providing ‘biocontrol services’ worth an estimated \$4 billion per year in the US alone (Losey & Vaughan, 2006), which is likely an underestimate (Landis *et al.*, 2008). Perennial habitats often support a greater abundance or diversity of natural enemies than annual crops (Schmidt & Tscharntke, 2005; Bianchi *et al.*, 2006; Werling & Gratton, 2008), in part because of reduced disturbance and stable supplies of food and shelter (Thomas *et al.*, 1991; Bommarco & Ekbom, 2000; Lee *et al.*, 2001). At the same time, habitats with diverse vegetation and complex structure may be more likely to contain limiting resources for natural enemies (Landis *et al.*, 2000; Langellotto & Denno, 2004). Past research has examined biocontrol services within a single, annual monocrop (soybean), showing that biocontrol could be negatively affected by biofuel-driven expansion of corn production in the landscape (Landis *et al.*, 2008). Here, we build on this work by examining the impact of local- and landscape-scale factors on natural enemies in potential biofuel crops ranging from an intensively managed, annual monoculture to diverse, perennial grasslands. First, we characterized the biomass and family richness of natural enemies at 40 corn, switchgrass and prairie sites across southern Michigan (Fig. 1; Dataset S1 in Supporting information). Next, we quantified the potential for predator communities in different habitats to control pests by measuring predation of eggs of a common crop pest [corn earworm, *Helicoverpa zea*, (Boddie) (Lepidoptera: Noctuidae)] at 60 corn, switchgrass and prairie sites in Michigan and Wisconsin (Dataset S2). We then related these variables to existing site- and landscape-level factors relevant to future biofuel production (Table 1), asking (1) do natural enemy biomass, family richness and egg predation vary between corn and perennial grasslands, (2) do they vary with forb cover and floral diversity, (3) are these response variables associated with changes in the area of annual and perennial habitats in the surrounding landscape and (4) are they affected by landscape heterogeneity?

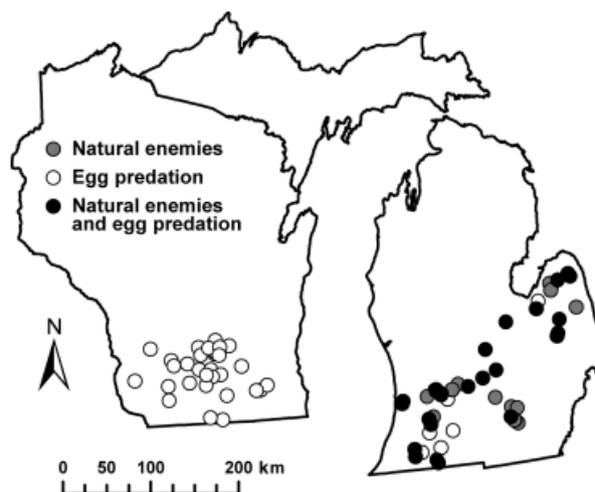


Fig. 1 Arthropod natural enemies and predation of pest eggs were sampled in corn, switchgrass and mixed prairie sites scattered across southern Wisconsin and Michigan (total $n = 78$). A subset of sites ($n = 22$) were used for sampling of both natural enemy communities and egg predation.

Materials and methods

Study sites

Arthropod natural enemies and predation of pest eggs were sampled in corn, switchgrass and mixed prairie communities in Michigan and Wisconsin (Fig. 1). Corn sites were conventionally managed on commercial farms and ranged from 3 to 121 ha in size. Switchgrass and prairie stands were managed for wildlife habitat or seed production and ranged from 2 to 101 ha. Arthropods were sampled in Michigan at 10 corn, 17 switchgrass and 13 prairie sites; nearest-neighbor distances for sites ranged from 0.24 to 44.6 km ($\bar{X} = 9.7$ km). For egg predation, ten sites of each habitat were located in southern Michigan and Wisconsin, for a total of $n = 20$ sites per crop type; nearest-neighbor distances ranged from 2.4 to 65.4 km ($\bar{X} = 14.5$ km).

Natural enemy biomass and family richness

Arthropod natural enemies were sampled at each site using sweep nets in June and July 2009. Once per month, a sampler walked to the center of each site and took two sets of 50 sweep samples walking in opposite directions away from the center (total of 100 sweeps per date, 200 for the season). Arthropods were identified to family (Borror *et al.*, 1992), with natural enemies defined as families known to prey on or parasitize arthropod herbivores. Natural enemy ‘family richness’ was quantified as the number of families captured per 200 sweeps. This provided a family-level

Table 1 Names and definitions of variables expected to impact arthropod natural enemy biomass, family richness and egg predation in three candidate biofuel crops (corn, switchgrass and mixed prairie). All landscape variables were calculated for a 1.5 km radius surrounding each site. Each represents a hypothesis generated from existing literature

Variable	Definition	Rationale for hypothesized impact
Crop	Binary variable, takes on a value of '0' for corn sites and '1' for grasslands	1. Perennial habitats provide a stable resource base*
ForbCover†	Mean cover-class of forbs in 0.25 m ² quadrats	2. Floristically diverse habitats more likely to contain key resources‡
FloralDiv	Total number of blooming plant species detected in monthly 100 m ² transects ($\log_{10}(x + 1)$ transformed)	3. See 2 above
HerbPerLS	Proportion of landscape composed of herbaceous, perennial habitats	4. See 1 above
ForestLS	Proportion of landscape in forest	5. See 1 above
AnnualLS	Proportion of landscape in annual crops	6. Annual crops may lack resources for predators§
AnnPerEdge	Length of edge (m) shared between annual and perennial habitats divided by total area of these habitats (ha)	7. Predators in heterogeneous landscapes benefit from juxtaposition of productive, ephemeral crops with less productive, stable habitats¶
SimpsonD	Simpson's diversity of terrestrial, vegetated habitats	8. Heterogeneous landscapes contain different habitats that provide complementary resources and/or support different predator species
Crop × landscape var.	Interactions between Crop and each landscape variable	9. The effect of local habitat conditions can depend on availability of resources in the surrounding landscape**

*Bianchi *et al.* (2006), Wissinger (1997).

†Different floristic variables were available for studies of different response variables: the ForbCover variable was measured at all sites where natural enemy biomass and family richness were measured, while FloralDiv was measured at sites where egg predation was quantified.

‡Bianchi *et al.* (2006), Haddad *et al.* (2009), Langellotto & Denno, (2004).

§Bianchi *et al.* (2006), Bommarco & Ekbom (2000), Landis *et al.* (2000).

¶Rand *et al.* (2006), Wissinger (1997).

||Dunning *et al.* (1992), Tschamtkke *et al.* (2007).

**Tschamtkke *et al.* (2005), Rundlof & Smith (2006).

metric of diversity analogous to species density (*sensu* Hurlbert, 1971) that should be positively related to the number of natural enemy families a pest might encounter in a given area of habitat. We also determined the length of a subset of specimens from each family to the nearest millimeter. We then used published length vs. mass relationships (Hodar, 1996) to convert abundance data to biomass (grams of natural enemy/200 sweeps). We used biomass, and not abundance, because it should scale more directly with the consumptive power of natural enemy communities given that taxa vary greatly in size (Saint-Germain *et al.*, 2007).

Measuring predation rates

We assayed the potential for predator communities at each site to consume pests by measuring predation of

eggs of corn earworm, *H. zea*, which is a pest of a variety of Midwestern crops including corn and tomato (Foster & Flood, 1995). Analysis of video taken at a limited number of sites suggested that corn earworm eggs are consumed by a taxonomically diverse suite of invertebrate predators and that predation of eggs is strongly related to predator activity (Fig. S1). Hence, removal of corn earworm eggs was used to provide a general index of the activity of a wide range of predators. Corn earworm eggs were obtained from a commercial insectary (French Agricultural Research, Lamberton, MN, USA); moths oviposited on paper discs cut from brown grocery bags. Standard-sized egg clusters were created by cutting paper discs into pieces containing approximately 50 eggs (range: 23–90). Egg clusters were then affixed to 5 × 6 cm pieces of cardstock using white, water-soluble glue (Fig. S2). The number of eggs per

'egg card' was counted and recorded. Eggs were freeze-killed prior to deployment to prevent hatching; freeze-killing did not affect egg consumption by a common predator in a lab test (Appendix S1).

Egg predation was measured at four sampling stations at each site during the weeks of 22 June and 20 July 2009. When possible, stations were located at least 50 m from habitat edges and 50 m apart. Stations were arranged in either a single, linear transect running down the center of the field (for narrow sites) or in two transects separated by 50 m and extending from the field edge towards the center (for large sites). Eggs were affixed to platforms that provided a standardized foraging substrate for predators (Fig. S2). Platforms consisted of either 30 × 30 cm pieces of 4 mm thick green plastic board (in Michigan; N. Glantz & Sons, Louisville, KY, USA) or a 30 × 30 cm piece of plywood painted a similar shade of green (in Wisconsin). Using different platform materials did not affect predation: the proportion of eggs removed was similar in Michigan ($\bar{X} = 0.36$, 95% C.I.: 0.27, 0.45) and Wisconsin ($\bar{X} = 0.40$, 95% C.I.: 0.29, 0.50). Platforms rested atop a 50 cm length of 2 cm diameter PVC placed over a 61 cm length of metal rebar pounded halfway into the ground. Two egg cards were affixed to the underside of each platform using thumbtacks (Fig. S2). One card was protected with a 100 mm diameter plastic petri dish, providing an estimate of egg removal in the absence of predators. A 4 cm diameter hole was melted into petri dishes using a soldering iron and covered with a piece of fine mesh (97 holes/cm², Skeeta Inc., Bradenton, FL USA) affixed with a hot glue gun to provide ventilation. Predator excluders were clamped over one egg card using 5 cm binder clips (Fig. S2). Egg cards were collected from the field after 48 h and the number of eggs remaining recorded. The proportion of eggs remaining at each station was calculated by dividing final by initial egg numbers. Average rates of egg predation, $EP_{avg,ij}$, were then quantified for all $i = 60$ sites on each date ($j = 1, 2$) by averaging across the $k = 4$ stations:

$$EP_{avg,ij} = \frac{\sum_k ED_{e,ijk}}{k} - \frac{\sum_k ED_{p,ijk}}{k}, \quad (1)$$

where $ED_{e,ijk}$ is the proportion of eggs that disappeared at the k^{th} station from egg cards that were exposed to predators and $ED_{p,ijk}$ is the disappearance rate for eggs protected by predator excluders. The variable $EP_{avg,ij}$ represents average rates of egg disappearance after accounting for factors besides predation. We took the mean of this measure across the two sample dates to get season-averaged egg predation.

Measuring plant diversity

Originally, corn and switchgrass stands were expected to be near-monocultures and prairies were expected to be polycultures. This categorical distinction between habitats was not a good representation of reality, as plant diversity varied considerably both within and between habitats (Table S1). For this reason, we treated plant diversity as a continuous variable. In specific, we measured variables that distinguished between sites dominated by the focal crop plant (corn or prairie grasses) and sites containing a mix of forb and grass species. For the arthropod community study, we estimated percent cover of forbs in five, 25 × 100 cm quadrats located in the site center and at random distances in each of the four cardinal directions (distances ranged from 8 to 50 m). Each quadrat was assigned to ordinal, Daubenmire cover classes (Daubenmire, 1959) based on percent cover of forbs (Classes were 1: <5% forb cover, 2: 5–25%, 3: 25–50%, 4: 50–75%, 5: 75–95%, and 6: 95–100%). The mean cover class was taken across the five quadrats to obtain an index of forb cover for each site.

For the egg predation study, we counted the number of flower species that were blooming in a single 1 × 100 m transect at each site in June, July and August, using cumulative species richness over the entire summer (hereafter 'floral diversity,' abbreviated as 'Floral-Div' in Table 1) as a measure of plant diversity. The first sample date was missed at six Michigan sites (three corn and three grassland, an additional sample date was missed at one of these corn sites), and flower data were not collected from Wisconsin corn sites because blooming plants were rare or non-existent. For Wisconsin corn sites, we set floral diversity to its median value (0) from Michigan. Importantly, the estimated effect of floral diversity on egg predation was similar regardless of whether these corn sites were included (slope for effect of flower diversity: $b = 0.17$, 95% C.I.: 0.016, 0.32) or excluded ($b = 0.15$, 95% C.I.: -0.0051, 0.31) from analysis. Floral diversity was $\log_{10}(x+1)$ transformed before analysis to linearize its relationship to egg removal, but was back-transformed for graphing (Fig. 4b). Both measures of plant diversity had considerably broader ranges in grassland (Figs 2b, 3b and 4b). Consequently, parameter estimates for effects of floral diversity and forb cover primarily predict variation in response variables across grassland sites.

Landscape variables

Expansion of biomass production could alter the landscape to affect ecosystem services (Table 1) (Landis *et al.*, 2008; Landis & Werling, 2010; Webster *et al.*, 2010). To address this, we derived landscape characteristics with-

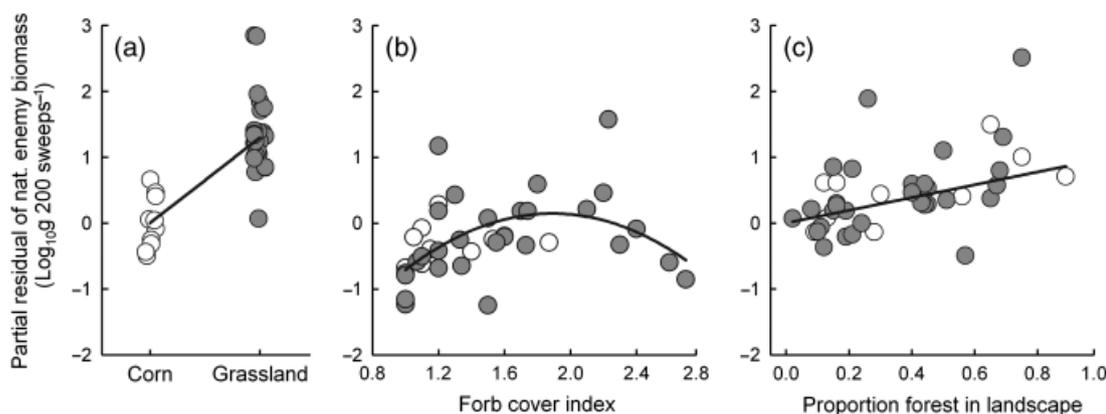


Fig. 2 Biomass of natural enemies was greater in perennial grasslands than corn and increased at sites with intermediate levels of forb cover that were surrounded by forest. Natural enemy biomass (a) was an order of magnitude higher in perennial grasslands (switchgrass and prairie, filled symbols) than corn (open symbols), (b) showed a hump-shaped relationship to forb cover and (c) increased with the proportion of forest in the landscape within a 1.5 km radius. Graphed values are partial residuals of $\log_{10}(\text{grams natural enemy biomass}/200 \text{ sweeps})$ obtained by adjusting for other factors in the AIC_c -best model (Table 2). Partial residuals for the i th observation, adjusted for all factors except x_j , are $e_i + b_j x_{ij}$ for (a, c) and $e_i + b_j x_{ij} + b_k (x_{ij})^2$ for (b), where e_i is the raw residual for the observation, b_j is the slope for the linear effect of x_j from the best model, and b_k is the slope for the quadratic effect of x_j . Residuals are on the original scale of the data. The regression line shows the effect of predictors based on the best model, graphed as (a, c) $y = b_j x_j$ and (b) $y = b_j x_j + b_k (x_{ij})^2$. Forb cover is the average Daubenmire cover class for forbs taken across five quadrats per site; higher values indicate greater percent cover of forbs. Jitter was added to points in (a) to reduce overlap.

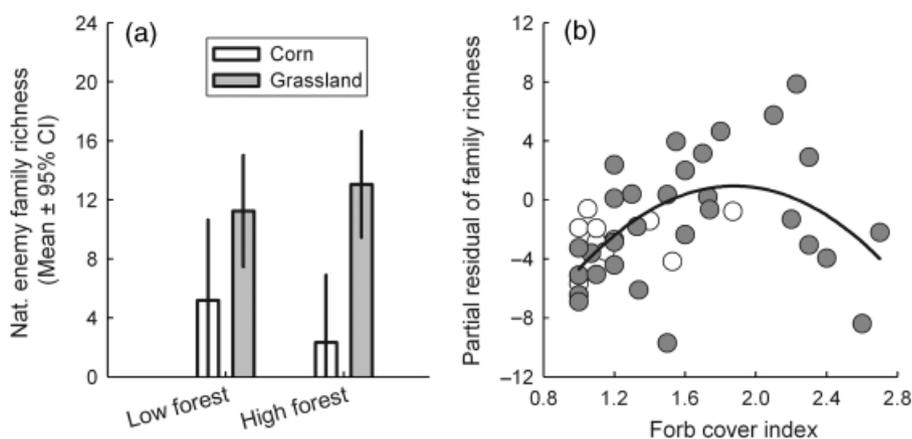


Fig. 3 More natural-enemy families were captured in perennial grasslands with intermediate levels of forb cover compared with corn. (a) Family richness (number of families/200 sweeps) of natural enemies was greater in grasslands (switchgrass and prairie, filled symbols) compared with corn (open symbols), a difference which was more pronounced in landscapes with extensive forest. Bars show predictions of the AIC_c -best model for sites surrounded by low (16% forest; 25th percentile of forest cover) and high areas of forest (52%; 75th percentile of forest cover) within 1.5 km (ForbCover held constant at 1.2). Error bars are 95% confidence intervals. (b) Family richness also showed a hump-shaped relationship to forb cover, peaking at intermediate levels. For (b), we graphed partial residuals of family richness after adjusting for other factors using the AIC_c -best model (Table 2). Partial residuals for the i th observation, adjusted for all factors except x_j , are $e_i + b_j x_{ij} + b_k (x_{ij})^2$; where e_i is the raw residual for the observation, b_j is the slope for the effect of x_j from the best model, and b_k is the slope for the quadratic effect of x_j ; residuals are on the original scale of the data. The regression line shows the predicted effect of forb cover based on the best model, graphed as $y = b_j x_j + b_k (x_{ij})^2$. Forb cover is the average Daubenmire cover class for forbs taken across five quadrats per site; higher values indicate greater percent cover of forbs.

in a 1.5 km radius of each study site using the 2009 Cropland Data Layer (CDL, 56 m resolution) (USDA, 2010). A comparison of this dataset to on-the-ground

data taken at a subset of sites suggests the CDL could distinguish landscapes based on characteristics of interest (Appendix S2). We reclassified the CDL in three

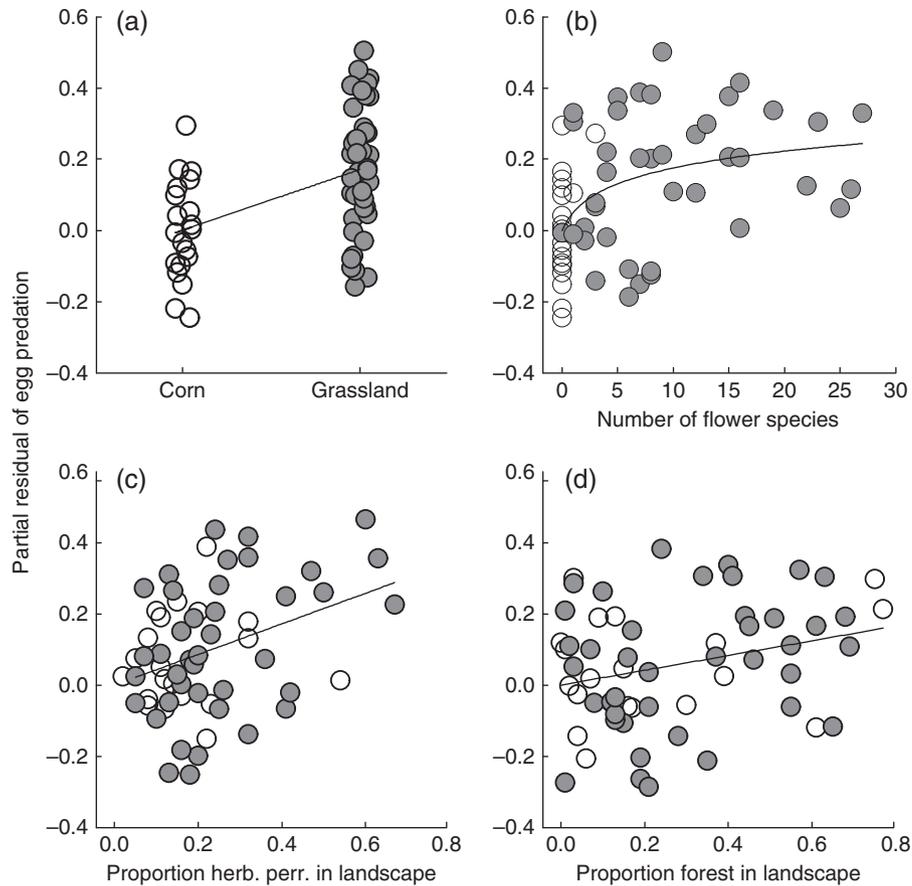


Fig. 4 Egg predation was greater in perennial grasslands compared with corn and was positively related to floral diversity and the area of perennial habitats in the landscape. The proportion of eggs removed by predators was greater in (a) perennial grasslands (switchgrass and prairie, filled symbols) compared with corn (open symbols), (b) increased with floral diversity and showed positive associations to (c) the area of herbaceous, perennial habitat and (d) forest within 1.5 km of sites. Partial residuals for the i th observation, adjusted for all factors except x_i , are $e_i + b_j x_{ij}$; where e_i is the raw residual for the observation and b_j is the slope for the effect of x_j from the best model; residuals are on the original scale of the data. The regression line shows the predicted effect of the variable of interest based on the best model (Table 3), graphed as $y = b_j x_j$. Floral diversity is the cumulative number of flower species found blooming across three, monthly 1×100 m transects at each site. Jitter was added to points in (a) to reduce overlap.

different ways to provide information on landscape composition and heterogeneity. The first reclassification was used to quantify composition and included four broad landscape classes. An 'annual agriculture' class contained 27 annual crops and was dominated by corn and soybean (85% of area; percentage based on cumulative area of each habitat across 1.5 km landscapes centered on all $n = 60$ sites used for egg predation studies). 'Herbaceous, perennial habitat' was dominated by hayfields and pasture (84%) but also included alfalfa, clover and wildflower fields, fallow agricultural land, shrublands, and unmanaged grassland. The 'forest' class was dominated by deciduous forest and wooded wetlands (97%) but also included coniferous and mixed forests. All other land cover classes were pooled into a fourth category not used in analyses. We

calculated the proportion of the landscape within 1.5 km of each site in these three cover types using ARCGIS 9.3 (ESRI, 2008). The second reclassification was used to quantify terrestrial habitat diversity and included twelve landcover types: corn, soybeans, small grains, flowering herbaceous crops, flowering woody crops, oil seeds, other crops, herbaceous perennial habitat (as in the first reclass), deciduous forest, coniferous forest, wetland, and vegetated urban land (<50% impervious surface). We used the Patch Analyst 4.0 extension to ARCGIS to calculate a modified Simpson's Diversity Index using the area of each of the 12 habitat classes for a 1.5 km radius around each site (Rempel, 2010). The third reclassification was used to measure the length of border shared between annual and perennial habitats. To accomplish this, we pooled all annual crops (as in the first

reclass) into one class, all seminatural perennial habitats (herbaceous perennial and forest) into a second class, and all other habitats into a third class. We then used contrast-weighted edge metrics from the Patch Analyst extension (Rempel, 2010) to calculate the density of borders between annual and perennial habitats (meters of shared edge per total area of annual and perennial habitats within 1.5 km). Means, ranges, and correlations between variables are in Table S2.

Data analysis

We modeled natural enemy biomass, family richness and pest egg removal as a function of several local and landscape characteristics (Table 1; Analyses S1 and S2). The modeling process began by entering all independent variables into a full, linear model. Next, all possible subsets of the full model were analyzed using the multimodel inference package, MuMin in R v. 2.10 (R Core Development Team, 2009; Barton, 2010). The most predictive model in the set was identified using bias-corrected Akaike's Information Criterion (AIC_c) and used for inference. Akaike weights (w) were also calculated for all models in the set; weights were then summed for all models containing the i th predictor variable. These 'variable weights' approximate the likelihood that the i th variable will appear in the best model in repeated runs of an experiment. They quantify support for a variable across the entire model set and allow the relative importance of all variables (including those not appearing in the best model) to be compared (Burnham & Anderson, 2002). We computed the Moran's I test for residual spatial autocorrelation (65 km distance band) for the best models using the spatial dependence package, spdep in R (Bivand *et al.*, 2010) and found no evidence of autocorrelation ($-0.07 \leq I \leq 0.02$; $P > 0.37$ for all tests).

For graphing, we used the AIC_c -best model to calculate partial residuals. These values show the residual effect of a predictor on response variables after accounting for effects of all other variables in the model while preserving the original scale of the data (Fox, 2008). Partial residuals for the i th observation, adjusted for all factors except x_j , were calculated as $e_i + b_j x_{ij}$ where e_i is the raw residual and b_j is the slope for the effect of x_j from the best model (Fox, 2008). Graphs of partial residuals were combined with the regression line $y = b_j x_{ij}$ to produce a 'component plus residual plot,' which shows the predicted relationship between each independent and dependent variable (Fox, 2008). When appropriate, we also used predicted means and confidence intervals to compare the relative magnitude of response variables in different habitats and landscapes; Working-Hotelling confidence intervals were used to

encompass the entire response surface (Neter *et al.*, 1996). Predictions were made at different values of the predictor of interest while holding covariates constant at values within the range of the dataset.

Results

Natural enemy biomass and family richness

Natural-enemy biomass was affected by biofuel crop type, forb cover and landscape-level perenniality (Fig. 2). The AIC_c -best model ($R^2 = 0.66$) predicted a more than order-of-magnitude increase in biomass (1.29 \log_{10} -units) in perennial grasslands compared with corn (Fig. 2a) and described a hump-shaped relationship between biomass and forb cover, with biomass increasing 0.86 \log -units to its peak at a forb-cover index of 1.89 (corresponding to 5–25% cover of forbs) (Fig. 2b, Table 2). In combination, these effects were associated with an increase in biomass of greater than two orders of magnitude in grasslands with intermediate levels of forb cover ($1.29 + 0.86 = 2.15 \log_{10}$ -units). The composi-

Table 2 Parameter estimates ($\beta \pm SE$) from the AIC_c -best model predicting natural enemy biomass and family richness in corn and perennial grasslands. Variable weights ($0 \leq w_+ \leq 1$) quantify relative support for each variable across the entire set of models, which contained all possible combinations of predictors

Parameter	Predator biomass		Family richness	
	$\beta \pm SE^*$	$w_+ \dagger$	$\beta \pm SE$	w_+
Intercept	-2.36 ± 0.26		8.91 ± 2.14	
Crop	1.29 ± 0.21	1.00	3.96 ± 2.39	1.00
ForbCover	0.80 ± 0.25	0.90	5.21 ± 1.61	0.80
ForbCover ²	-1.08 ± 0.38	0.84	-7.30 ± 2.48	0.75
HerbPerLS		0.23		0.26
ForestLS	0.97 ± 0.38	0.60	-7.99 ± 3.98	0.47
AnnualLS		0.39		0.48
AnnPerEdge		0.25		0.31
SimpsonD		0.30		0.34
Crop \times HerbPerLS		0.04		0.06
Crop \times ForestLS		0.11	13.00 ± 5.04	0.32
Crop \times AnnualLS		0.07		0.25
Crop \times AnnPerEdge		0.04		0.07
Crop \times SimpsonD		0.07		0.13

*Blank spaces indicate a parameter was not included in the AIC_c -best model.

†Variable weights obtained by summing w for all models in the set that included a given variable; weights approximate the likelihood a given variable will be included in the best model in repeated runs of an experiment.

tion of the surrounding landscape also mattered: the best model predicted an exponential increase in natural enemy biomass with the area of forest in the surrounding landscape (Fig. 2c, Table 2). These effects received moderate to strong support across the entire model set ($w_+ \geq 0.60$; Table 2). In contrast, variable weights provided minimal support for predictors describing landscape heterogeneity or interactions between crop type and landscape context ($w_+ \leq 0.30$; Table 2).

Family richness of predators was greater in perennial grasslands with intermediate amounts of forb cover (Fig. 3). The best model ($R^2 = 0.69$) contained an interaction between crop type and area of forest in the landscape (Table 2), predicting that positive differences in family richness between grasslands and corn were greater in forested landscapes (Fig. 3a). Variable weights provided strong support for a main effect of crop type ($w_+ = 1.00$), but minimal support for its interaction with forest cover ($w_+ = 0.34$), suggesting this interaction was not consistently included in the most predictive models. As for biomass, the best model described a hump-shaped relationship between family richness and forb cover (Fig. 3b), which was strongly supported across the entire model set ($w_+ \geq 0.75$). The combined effects of crop type and forb cover on family richness were substantial. For example, the model predicted a fourfold increase in family richness in grasslands with a median cover of forbs ($\bar{X} = 14$ families; 95% CI: 11, 18; median forb cover = 1.5) compared with corn, which contained very low forb cover ($\bar{X} = 3$ families; 95% CI: -1, 8; median forb cover = 1.1; ForestLS held constant at median value). Variable weights provided minimal support for predictors describing landscape heterogeneity or interactions between crop type and landscape context ($w_+ \leq 0.34$; Table 2).

Egg predation

Data provided strong support for crop type, floral diversity, and landscape-level perenniality as predictors of egg predation (Table 3). The AIC_c-best model ($R^2 = 0.59$) predicted greater egg predation in perennial grasslands compared with corn (Fig. 4a) and indicated a positive association with floral diversity (Fig. 4b, Table 3). Data suggest these factors were associated with substantial increases in egg predation in moderately diverse grasslands. For example, the best model predicted threefold greater predation in grasslands with median floral diversity (Proportion eggs predated: $\bar{X} = 0.47$; 95% CI: 0.35, 0.58; median of eight flower species) compared with corn ($\bar{X} = 0.13$; 95% CI: 0.004, 0.27; median of 0 flower species; landscape predictors held at median levels). The composition of the sur-

Table 3 Parameter estimates ($\beta \pm SE$) from the AIC_c-best model predicting egg predation in corn and perennial grasslands. Variable weights ($0 \leq w_+ \leq 1$) quantify relative support for each variable across the entire set of models, which contained all possible combinations of predictors

Model term	$\beta \pm SE^*$	$w_+ \dagger$
Intercept	0.015 \pm 0.055	
Crop	0.171 \pm 0.080	0.91
Log ₁₀ (FloralDiv + 1)	0.168 \pm 0.076	0.80
HerbPerLS	0.429 \pm 0.163	0.87
ForestLS	0.207 \pm 0.106	0.58
AnnualLS		0.35
AnnPerEdge		0.29
SimpsonD		0.31
Crop \times HerbPerLS		0.31
Crop \times ForestLS		0.13
Crop \times AnnualLS		0.09
Crop \times AnnPerEdge		0.06
Crop \times SimpsonD		0.08

*Blank spaces indicate a parameter was not included in the AIC_c-best model.

†Variable weights obtained by summing w for all models in the set that included a given variable; weights approximate the likelihood a given variable will be included in the best model in repeated runs of an experiment.

rounding landscape was also an important predictor of egg predation: predation within a patch increased with the area of herbaceous-perennial and forest habitat in the landscape (Fig. 4c and d; Table 3). Landscape impacts were also large: egg predation in grasslands was predicted to increase almost twofold from 0.30 (95% CI: 0.09, 0.51) to 0.56 (95% CI: 0.26, 0.87) as the area of herbaceous, perennial habitat in the landscape increased to its maximum (Other variables held constant: FloralDiv = 1, ForestLS = 0.19). Accordingly, variable weights provided strong support for effects of crop, floral diversity, and area of herbaceous perennials in the landscape ($w_+ \geq 0.80$), moderate support for an effect of forest cover ($w_+ = 0.58$) and minimal support for landscape heterogeneity and interactions between crop type and landscape variables ($w_+ \leq 0.31$; Table 3).

Discussion

Our results suggest that local- and landscape-scale conditions will combine to affect biocontrol services in biofuels. At a local-scale, perennial grasslands could support greater biocontrol services compared with corn (Figs 2a, 3a and 4a), a benefit which may increase in grasslands incorporating modest amounts of forb cover and floral diversity (Figs 2b, 3b and 4b). At a broader scale, our data suggest that biocontrol services within a

crop field will depend on its position within the landscape, increasing in fields surrounded by perennial habitats (Figs 2c and 4c, d). Interestingly, the combined effects of local- and landscape-level conditions were generally additive, with minimal support for interactive effects (Tables 2 and 3). In the one case where an interactive effect occurred in the best model, it indicated that the magnitude, but not direction, of differences between grasslands and corn varied between landscapes (Fig. 3a). This suggests that the local benefits of perennial grasslands for biocontrol services may hold across a variety of landscape contexts. Importantly, the grasslands that were sampled were not managed for biofuel production. Examining how local management moderates biocontrol benefits is an important goal for future research (Landis & Werling, 2010).

Research detailed here also supports the hypothesis that changes in the composition and diversity of primary producers cascade to affect the structure and function of higher trophic levels (Haddad *et al.*, 2009). Specifically, natural enemy biomass and richness (structure) and egg predation (function) increased over low to moderate levels of forb cover and flower diversity, respectively (Figs 2b, 3b and 4b). These results, collected over a large region, corroborate a considerable body of plot-scale work on the benefits of polycultures (Andow, 1991). Intriguingly, we found that natural enemy biomass and family richness peaked at intermediate levels of forb cover (Figs 2b and 3b). If true, this suggests they can be maintained at relatively high levels by incorporating only moderate amounts of forbs into biofuel grasslands. We also observed a decline in natural enemy biomass and richness at high levels of forb cover (Figs 2b and 3b). One possibility is that natural enemy biomass and richness initially increase as forb-based resources increase, but then decline as increasing forb cover reduces the availability of some other, unknown resource. It is important to acknowledge that other biotic and abiotic factors likely covaried with forb cover and diversity across the study region. Disentangling forb cover and diversity from associated changes in other site and plant community attributes will help target causal variables that can be manipulated in biofuel plantings.

The landscape effects documented in this study suggest that expansion of biofuel production could affect biocontrol services by driving changes in the area of perennial habitats. For example, decreasing the area of perennial habitats by converting forests or grasslands to *intensely managed*, annual crops like corn could cause associated declines in biocontrol, while planting annual cropland with perennial feedstocks could increase it (Fig. 2c and Fig. 4c and d). This hypothesis is supported by studies from a variety of crops that have found

positive correlations between predation and parasitism and the area of perennial habitat in the surrounding landscape (Bianchi *et al.*, 2006). A key caveat is that, although existing perennial habitats are a broad mixture of managed (hay fields, wood lots) and unmanaged (prairie and forest preserves) habitats, they are not currently under management for biomass production. It will be important to measure service rates in biofuels and other crops set in experimental landscapes that vary in the area of novel biofuel crops, which may be very different from existing perennial habitats.

Results suggest that landscape composition, but not heterogeneity, affected biocontrol potential. Specifically, the area of perennial habitats was an important predictor of all response variables, while landscape heterogeneity was not (Tables 2 and 3). Perennial habitats may provide limiting resources that are largely absent from landscapes dominated by annual crops (Bianchi *et al.*, 2006). As a result, the dichotomy between landscapes dominated by resource-poor annual crops and those containing perennial habitats may be more important than changes in the diversity or interspersion of cover types. Importantly, this does not mean that heterogeneity in other landscape properties or at other scales is not important. It is possible that differences among the landscape cover-classes used in this study did not capture heterogeneity in factors that are actually important to natural enemies. In addition, the apparent importance of heterogeneity can vary depending on the resolution of landscape data (Chust *et al.*, 2003), which was limited to 3136 m² in this study.

Arthropod natural enemies could provide valuable services by minimizing the impact of pests on yield and reducing the need for costly insecticide applications (Landis *et al.*, 2008). However, the impact of pests (and hence the need for biological control) on biomass in novel production systems is relatively unknown (Landis & Werling, 2010). A meta-analysis found that trophic cascades were highly variable in grasslands, suggesting that changes in predation may not consistently cascade to affect plant biomass (Halaj & Wise, 2001). It will be important to complete a full assessment of the value of biocontrol services in grasslands and other production systems, which will require measuring the ultimate impact of predators on biomass yields and insecticide use.

A diverse body of research suggests that biofuel landscapes incorporating perennial grasslands could produce multiple ecosystem services at greater rates than landscapes dominated by existing, annual monocrops. Grasslands can support a greater abundance and diversity of birds of conservation concern (Fletcher *et al.*, 2010), sequester soil carbon (Pineiro *et al.*, 2009), mitigate disservices by reducing surface runoff into

streams (Lee *et al.*, 2003), and support organisms important for biological control (Thomas *et al.*, 1991; Gardiner *et al.*, 2010). Furthermore, diverse grasslands could produce higher yields on poor soils relative to monocultures, without the need for fertilizer (Tilman *et al.*, 1996), reducing inputs and yielding greater net greenhouse gas and energy benefits (Tilman *et al.*, 2006; Fargione *et al.*, 2008). However, productive monocultures (e.g., of corn or switchgrass) are expected to produce more biomass (and consequently greater net revenue) than diverse feedstocks such as mixed prairie (Schmer *et al.*, 2008; James *et al.*, 2010). This suggests that there are considerable opportunities and challenges associated with biofuel production (Fargione *et al.*, 2009). On the one hand, non-marketable services could decline if landscapes are maximized for commodity production using existing annual crops (Landis *et al.*, 2008) and disservices could increase (Donner & Kucharik, 2008). On the other hand, policy-makers could explicitly include non-marketable services and disservices in decision making and create incentives for farmers to cultivate crops that jointly produce biomass, support biodiversity and minimize negative environmental impacts (Fargione *et al.*, 2009). Quantifying the response of services to land use change, identifying tradeoffs, examining their magnitude under different land use scenarios, and placing value on ecosystem services are key tasks that will enable society to make informed decisions that take both marketable and non-marketable services into account (Kareiva *et al.*, 2007; Steffan-Dewenter *et al.*, 2007; Swinton *et al.*, 2007; Daily *et al.*, 2009; Nelson *et al.*, 2009; Power, 2010).

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References

Andow DA (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology*, **36**, 561–586.

- Barton K (2010) *Package 'MuMIn'*, R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://mumin.r-forge.r-project.org/> (accessed 15 November 2010).
- Bianchi F, Booij CJH, Tschamntke T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1715–1727.
- Bivand R, Altman M, Anselin L *et al.* (2010) *Package 'spdep'*, R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org/> (accessed 15 November 2010).
- Bommarco R, Ekbom B (2000) Landscape management and resident generalist predators in annual crop systems. In: *Interchanges of Insects Between Agricultural and Surrounding Landscapes* (eds Ekbom B, Irwin M, Robert Y), Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Borror DJ, Triplehorn CA, Johnson NF (1992) *An Introduction to the Study of Insects*. Harcourt Brace College Publishers, Fort Worth, TX, USA.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer, New York City, NY, USA.
- Chust G, Pretus JL, Ducrot D, Bedòs A, Deharveng L (2003) Identification of landscape units from an insect perspective. *Ecography*, **26**, 257–268.
- Daily GC, Polasky S, Goldstein J *et al.* (2009) Ecosystem services in decision making: time to deliver. *Frontiers in Ecology and the Environment*, **7**, 21–28.
- Daubenmire R (1959) A canopy-coverage method of vegetational analysis. *Northwest Science*, **33**, 43–64.
- Donner SD, Kucharik CJ (2008) Corn-based ethanol production compromises goal of reducing nitrogen export by the Mississippi River. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4513–4518.
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.
- ESRI (2008) *ArcGIS*. ESRI, Redlands, CA.
- European Parliament (2009) Directive 2009/28/EC of the European Parliament and of the Council of 23 April 2009 on the promotion of the use of energy from renewable sources and amending and subsequently repealing Directives 2001/77/EC and 2003/30/EC. *Official Journal of the European Union*, L140/39.
- Fargione J, Hill J, Tilman D, Polasky S, Hawthorne P (2008) Land clearing and the biofuel carbon debt. *Science*, **319**, 1235–1238.
- Fargione JE, Cooper TR, Flaspohler DJ *et al.* (2009) Bioenergy and wildlife: threats and opportunities for grassland conservation. *Bioscience*, **59**, 767–777.
- Fletcher RJ, Robertson BA, Evans J, Doran PJ, Alavalapati JRR, Schemske D (2010) Biodiversity conservation in the era of biofuels: risks and opportunities. *Frontiers in Ecology and the Environment*. doi:10.1890/090091.
- Foster R, Flood B (eds). (1995) *Vegetable Insect Management with Emphasis on the Midwest*. Meister Publishing Company, Willoughby, OH, USA.
- Fox J (2008) *Applied Regression Analysis and Generalized Linear Models*. Sage Publications Inc., Los Angeles, CA, USA.

- Gardiner MA, Tuell JK, Isaacs R, Gibbs J, Ascher JS, Landis DA (2010) Implications of three biofuel crops for beneficial arthropods in agricultural landscapes. *Bioenergy Research*, **3**, 6–19.
- Glover JD, Culman SW, DuPont ST *et al.* (2010) Harvested perennial grasslands provide ecological benchmarks for agricultural sustainability. *Agriculture, Ecosystems and Environment*, **137**, 3–12.
- Grandy AS, Robertson GP (2007) Land-use intensity effects on soil organic carbon accumulation rates and mechanisms. *Ecosystems*, **10**, 58–73.
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, **12**, 1029–1039.
- Halaj J, Wise DH (2001) Terrestrial trophic cascades: how much do they trickle? *The American Naturalist*, **157**, 262–281.
- Herkert JR (2009) Response of bird populations to farmland set-aside programs. *Conservation Biology*, **23**, 1036–1040.
- Hodar JA. (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica*, **17**, 421–433.
- Hooper DU, Chapin FS, Ewel JJ *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.
- James LK, Swinton SM, Thelen KK (2010) Profitability analysis of cellulosic energy crops compared with corn. *Agronomy Journal*, **102**, 675–687.
- Kareiva P, Watts S, McDonald R, Boucher T (2007) Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science*, **316**, 1866–1869.
- Landis DA, Gardiner MA, Van Der Werf W, Swinton SM (2008) Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 20552–20557.
- Landis DA, Werling BP (2010) Arthropods and biofuel production systems in North America. *Insect Science*, **17**, 1–17.
- Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, **45**, 175–201.
- Langelotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.
- Lee JC, Menalled FB, Landis DA (2001) Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *Journal of Applied Ecology*, **38**, 472–483.
- Lee KH, Isenhardt TM, Schultz RC (2003) Sediment and nutrient removal in an established multi-species riparian buffer. *Journal of Soil and Water Conservation*, **58**, 1–8.
- Losey J, Vaughan M (2006) The economic value of ecological services provided by insects. *Bioscience*, **56**, 311–323.
- Nelson E, Mendoza G, Regetz J *et al.* (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, **7**, 4–11.
- Neter J, Kutner M, Wasserman W, Nachtsheim C (1996) *Applied Linear Statistical Models*. McGraw-Hill, Boston, MA, USA.
- Pineiro G, Jobbagy EG, Baker J, Murray BC, Jackson RB (2009) Set-asides can be better climate investment than corn ethanol. *Ecological Applications*, **19**, 277–282.
- Power AG (2010) Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2959–2971.
- R Core Development Team (2009) *R: A language and environment for statistical computing*, Vienna, Austria, R Foundation for Statistical Computing. Available at: <http://www.R-project.org> (accessed 15 November 2010).
- Rand TA, Tylianakis JM, Tscharntke T (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters*, **9**, 603–614.
- Rempel R (2010) *Patch Analyst 4.2*, Thunder Bay, Ontario Canada, Centre for Northern Forest Ecosystem Research. Available at: <http://flash.lakeheadu.ca/~rrempe/patch/> (accessed 1 October 2010).
- Renewable Fuel Association (2010) *Climate of Opportunity: 2010 Ethanol Industry Outlook*. Renewable Fuels Association, Washington, DC, USA.
- Robertson GP, Dale VH, Doering OC *et al.* (2008) Agriculture – Sustainable biofuels redux. *Science*, **322**, 49–50.
- Robertson GP, Paul EA, Harwood RR (2000) Greenhouse gases in intensive agriculture: contributions of individual gases to the radiative forcing of the atmosphere. *Science*, **289**, 1922–1925.
- Rundlof M, Smith HG (2006) The effect of organic farming on butterfly diversity depends on landscape context. *Journal of Applied Ecology*, **43**, 1121–1127.
- Saint-Germain M, Buddle CM, Larrivee M *et al.* (2007) Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *Journal of Applied Ecology*, **44**, 330–339.
- Sanderson MA, Adler PR (2008) Perennial forages as second generation bioenergy crops. *International Journal of Molecular Sciences*, **9**, 768–788.
- Schmer MR, Vogel KP, Mitchell RB, Perrin RK (2008) Net energy of cellulosic ethanol from switchgrass. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 464–469.
- Schmidt MH, Tscharntke T (2005) The role of perennial habitats for Central European farmland spiders. *Agriculture Ecosystems & Environment*, **105**, 235–242.
- Sissine F (2007) *Energy Independence and Security Act of 2007: A Summary of Major Provisions.*, Congressional Research Service. CRS report no. RL34294. Available at: http://energy.senate.gov/public/_files/RL342941.pdf (accessed 30 July 2010).
- Steenwerth KL, Jackson LE, Calderon FJ, Stromberg MR, Scow KM (2002) Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. *Soil Biology & Biochemistry*, **34**, 1599–1611.
- Steffan-Dewenter I, Kessler M, Barkmann J *et al.* (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 4973–4978.
- Swinton SM, Lupi F, Robertson GP, Hamilton SK (2007) Ecosystem services and agriculture: cultivating agricultural ecosystems for diverse benefits. *Ecological Economics*, **64**, 245–252.

- Thomas MB, Wratten SD, Sotherton NW (1991) Creation of island habitats in farmland to manipulate populations of beneficial arthropods – predator densities and emigration. *Journal of Applied Ecology*, **28**, 906–917.
- Tilman D, Hill J, Lehman C (2006) Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, **314**, 1598–1600.
- Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.
- Tscharntke T, Bommarco R, Clough Y *et al.* (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, **43**, 294–309.
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*, **8**, 857–874.
- USDA (2010) *2009 Cropland Data Layer*. National Agricultural Statistics Service, Washington, DC, USA.
- Van Buskirk J, Willi Y (2004) Enhancement of farmland biodiversity within set-aside land. *Conservation Biology*, **18**, 987–994.
- Webster CR, Flaspohler DJ, Jackson RD, Meehan T, Gratton C (2010) Diversity, productivity and landscape-level effects in North American grasslands managed for biomass production. *Biofuels*, **1**, 451–461.
- Werling BP, Gratton C (2008) Influence of field margins and landscape context on ground beetle diversity in Wisconsin (USA) potato fields. *Agriculture Ecosystems & Environment*, **128**, 104–108.
- Wissinger SA (1997) Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biological Control*, **10**, 4–15.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Removal of pest eggs (*Helicoverpa zea*) provides an index of activity of a taxonomically diverse suite of predators. We used video cameras to observe diurnal and nocturnal predation of pest eggs (*Helicoverpa zea*) at four sampling stations over 48 h in one corn and prairie site in August 2009 (Ingaham County, MI). Invertebrates feeding on eggs came from two phyla (Arthropoda and Mollusca) containing three classes (Arachnida, Insecta and Gastropoda) and five orders (Araneae, Coleoptera, Hemiptera, Orthoptera and Pulmonata). Egg removal was positively related to predator activity, quantified as 'invertebrate hours' (product of the number of individuals in contact with eggs and the duration of each contact). Consequently, we expected egg removal to provide a direct measure of the activity of a wide variety of predators, supporting its use as a metric of predation in our multi-state study. Statistics are from a simple, bivariate linear regression of egg removal on invertebrate activity.

Figure S2. Removal of pest eggs was monitored on 'egg cards' attached to the underside of 30 × 30 cm platforms that provided a standardized foraging surface for predators; four were placed in each site. The pictured platform was held upside down for photographing. Eggs of *Helicoverpa zea* were oviposited on brown paper. Pieces of paper with approximately 50 eggs were cut out and glued to 5 × 6 cm pieces of cardstock using white glue. Egg cards were then affixed to the platform with thumbtacks. The egg card on the right is covered with a 'predator excluder' consisting of a petri dish with a mesh-covered ventilation hole, clamped to the platform using 5 cm binder clips.

Table S1. List of plant species encountered in corn ('CO'), switchgrass ('SW'), and mixed prairie ('PR'), including minimum, maximum and total number of species.

Table S2. Minimum ('Min'), median ('Med') and maximum values ('Max') of continuous variables for studies of natural enemy biomass and richness and egg predation along with Spearman rank correlations between all pairs of variables; units and definitions of variables are in Table 1 in the text.

Appendix S1. We conducted a simple lab experiment to determine if freeze-killing *Helicoverpa zea* eggs affected consumption by a common predator *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae). Discs (19 mm diameter) containing exactly 50 eggs were cut from paper towel (used as an oviposition substrate). Eggs were then either stored at below-freezing temperatures or at 10 °C for 72 h. *C. maculata* were collected from the field, placed in 100 mm diameter petri dishes with moist dental wick, and starved for 72 h. Individuals were then either given freeze-killed ($n = 6$) or live eggs ($n = 7$) and placed in a growth chamber (15:9 Light:Dark, 24 °C day, 18 °C night). After 24 h, *C. maculata* had consumed 100% of eggs in all replicates, regardless of treatment.

Appendix S2. Landcover data from the Cropland Data Layer ('CDL') (USDA, 2010) were compared to ground-truthed landcover data available for the $n = 30$ Michigan sites used in the egg predation study to determine if the CDL adequately characterized landscape composition. Specifically, we calculated the proportional area of herbaceous-perennial habitat, forest, and annual agriculture using both datasets for a 1.5 km radius around each site. We then used simple linear regression to determine if inter-site variability in ground-truthed data was reflected in the CDL. Results suggest that variability in the area of each cover type in the CDL dataset reflected reality on-the-ground (Annual ag: $R^2 = 0.98$, Forest: $R^2 = 0.92$, Herbaceous perennial: $R^2 = 0.71$). Further, slopes suggest a one-to-one relationship between area of a cover type in the CDL and ground-truthed data, suggesting that the CDL was not significantly over- or under-sampling cover types (Annual ag: $b = 0.98$, 95% C.I.: 0.93, 1.04; Forest: $b = 0.93$, 95% C.I.: 0.82, 1.04; Herbaceous perennial: $b = 0.82$, 95% C.I.: 0.62, 1.02). Note, for ground-truthed data 11% of the land area was not visible from roads and could not be classified; data for these patches were eliminated from this analysis.

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