Influence of habitat and landscape perenniality on insect natural enemies in three candidate biofuel crops

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ABSTRACT

Cultivation of biofuel crops could change agricultural landscapes, affecting natural enemies at multiple scales. We sampled five natural enemy families with sticky cards in three model biofuel habitats (corn, switchgrass and prairie; $n = 60$) across southern Michigan and Wisconsin, comparing captures between habitats and relating them to the area of forest, annual crop and herbaceous perennial habitat in the landscape within 2 km of sites. In a first analysis, we compared Coccinellidae assemblages between habitats and examined the impact of habitat type and landscape composition on species richness and abundance. Results showed that, at the habitat scale, perennial grasslands supported a greater abundance of uncommon, native coccinellids and hosted distinct species assemblages compared to corn. At a broader scale, abundances of exotic and uncommon native ladybeetles responded differently to landscape composition, decreasing with the area of herbaceous perennials and annual crops, respectively. In a second analysis, we related family-level abundances of Anthocoridae, Syrphidae, Dolichopodidae and Chrysopidae to habitat type and landscape composition. Dolichopodids were more abundant in grasslands, while anthocorid and syrphid abundance increased over fivefold with the area of herbaceous, perennial habitat in the landscape surrounding corn, but not grassland, sites. These findings suggest that perennial grasslands used for bioenergy production could conserve natural enemies which are less abundant in corn, the dominant biofuel in existing landscapes. Moreover, cultivating annual cropland with herbaceous, perennial habitats could affect the abundance of natural enemies in existing crops and alter the suitability of entire landscapes for these beneficial taxa.

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1. Introduction

Natural enemies live in dynamic agricultural landscapes that change as cultivation of existing crops responds to commodity prices and new cropping systems are introduced. These changes can affect natural enemies at local scales, as certain crops may provide more suitable habitat than others (Maredia et al., 1992a; Bommarco, 1999; Landis et al., 2000), and at the landscape scale, where changes in the area of key landscape elements can affect their abundance in crop habitats (Bianchi et al., 2006). The expansion of bioenergy production will introduce novel crops into agricultural landscapes and change the area of existing crops, causing changes at both these scales. Specifically, biofuel production could be based on crops ranging from annual monocultures like corn to perennial grasses grown in monoculture or as a part of diverse native communities (Sanderson and Adler, 2008; Renewable Fuels Association, 2010). At local scales, choices between these different crops may affect the suitability of individual crop

fields for different natural enemies (Gardiner et al., 2010). At broader scales, the abundance of natural enemies in these crops may depend on the area of different habitats that exist in the surrounding landscape (Bianchi et al., 2006; Werling et al., 2011), which are likely to change as biofuel production expands (Landis et al., 2008). Here, we build on past work by simultaneously examining the effects of habitat type and landscape composition on insect natural enemies in three biofuel crops. Understanding these relationships could allow cropping systems to be managed to conserve natural enemies (Landis and Werling, 2010).

Biofuel-driven changes in natural enemy communities could be important from both functional and conservation perspectives. From a functional perspective, different natural enemies attack different pests (Flint et al., 1998). Consequently, cultivation of different biofuel crops could affect natural biocontrol by changing the types of natural enemies that are abundant in the landscape. From a conservation perspective, the species richness of predator assemblages can depend on both local habitat conditions and the structure of the surrounding landscape (Attwood et al., 2008; Werling and Gratton, 2008). In addition, the species that comprise these assemblages can change over time as exotic taxa are introduced.

For example, ladybeetle (Coleoptera: Coccinellidae) assemblages in the Great Lakes region of the Midwestern US are now dominated by exotic invaders such as *Harmonia axyridis* (Pallas) and *Coccinella septempunctata* L., leading to concern that exotics will displace native species on the landscape (Harmon et al., 2006). In this context, past research has tested the hypothesis that non-crop habitats will become increasingly important for native taxa as exotics deplete prey within crops (Evans, 2004; Finlayson et al., 2008) and that exotic and native taxa respond differently to landscape composition (Gardiner et al., 2009a). Here, we combine these perspectives to simultaneously examine how habitat type and landscape composition affect the abundance of exotics and natives in biofuel crops.

Local- and landscape-conditions could combine in different ways to shape natural enemy assemblages in biofuel landscapes. Past research has shown that perennial habitats can support a greater abundance or diversity of natural enemies than annual crops, and that vegetational diversity can affect natural enemy abundances (Andow, 1991; Schmidt and Tscharntke, 2005; Werling et al., 2011). At broader scales, natural enemies are often more abundant or diverse in landscapes with abundant perennial habitat (Bianchi et al., 2006; Werling and Gratton, 2008). This suggests that biofuel patches and landscapes composed of perennial grasslands may support different natural enemy assemblages than those composed of annual crops. In addition, local- and landscape-scale conditions could interact, such that the effect of landscape composition varies between different habitats (and vice versa) (Thies and Tscharntke, 1999; Werling and Gratton, 2008). Given the recent interest in biomass production systems, we set out to examine how natural enemies will be affected by expanded production of annual bioenergy crops versus alternatives like perennial grasslands. To test for these effects, we sampled natural enemies with sticky cards in corn, switchgrass and prairie habitats ($n = 60$) across southern Michigan and Wisconsin and quantified the area of annual and perennial habitats in the surrounding landscape. We then examined how habitat type and landscape composition affect key insect natural enemies. A first set of analyses focused on the Coccinellidae, a functionally important group of natural enemies (Iperti, 1999). First, we compared the composition of coccinellid assemblages in the three biofuel crops. Next, we examined how habitat type and landscape composition combine to affect the species richness of these assemblages and the relative abundance of exotic and native ladybeetles. Finally, we extended this analysis to a wider variety of natural enemies by relating the abundance of four additional natural enemy families to habitat type and landscape composition. We predicted that (1) grasslands would support more diverse coccinellid assemblages than corn, (2) that grasslands would favor native coccinellids at both local and landscape scales, (3) that natural enemy abundance would be greater in grasslands and (4) that it would increase with the area of perennial habitats in the surrounding landscape.

2. Materials and methods

2.1. Study sites and sampling

Corn (*Zea mays* L.), switchgrass (*Panicum virgatum* L.), and prairie sites (mixed grasses and forbs) were sampled for predatory insects across southern Michigan and Wisconsin, USA (Fig. 1). Corn sites were commercially managed for grain or silage and ranged from 3 to 121 ha in size. Most farmers relied on seed treatments and/or transgenic resistance to manage corn pests and did not spray insecticide. For example, in Michigan only one farmer sprayed their corn with insecticides. Switchgrass and prairie sites were 2–101 ha in size, were managed for wildlife or seed
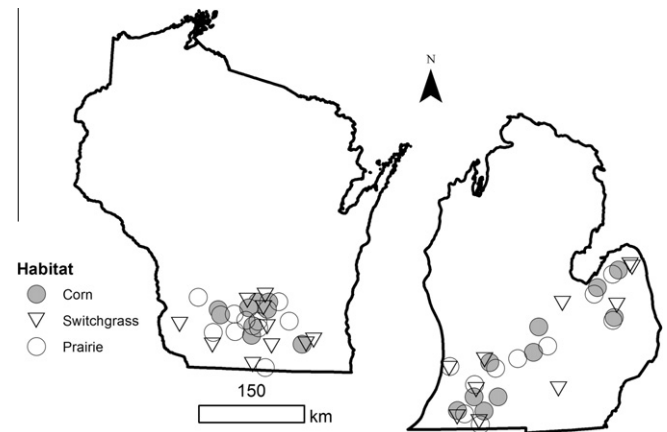

Fig. 1. Sticky cards were used to sample predatory insects in the families Coccinellidae, Anthocoridae, Syrphidae, Dolichopodidae, and Chrysopidae in corn, switchgrass and mixed prairie sites across southern Wisconsin and Michigan ($n = 10$ sites of each habitat per state; total $n = 60$).

production, and were never sprayed with insecticides. On average, sites were 9.7 km from the nearest neighboring site (range: 0.24–44.6 km). Data on the composition of vegetation are in Werling et al. (2011). Importantly, switchgrass sites were at times invaded with weeds and were not always true monocultures. However, they were still dominated by switchgrass (Mean % total biomass composed of *P. virgatum* at the 10 Michigan switchgrass sites: 98%, SE = 1.7; data from biomass collections in 4, 1 m^2 plots per site).

In summer 2009, we established four sampling stations at each site. Stations were 50 m apart and, when possible, at least 50 m from site edges. Stations were arranged in either a single, linear transect extending perpendicular from the field edge (for narrower sites) or in a 50×50 m square, with two traps 50 m from the edge and two 100 m away (for larger sites). At each station, a 23 by 28 cm unbaited, yellow sticky card (PHEROCON AM, Great Lakes IPM, Vestaburg, MI) was folded in half and attached to a 1.2 m tall white step-in poly fence post (Tractor Supply Co., Brentwood, TN) such that the bottom edge was approximately 1 m above the ground. Yellow sticky cards are an efficient way to capture Coccinellidae and other natural enemies (Maredia et al., 1992b; Stephens and Losey, 2004). Traps were changed weekly during summer 2009, with the first collection date on 8 and 15 June and the last collection date on 8 and 4 August 2009 in Michigan and Wisconsin, respectively (total of eight and nine collection weeks in the two states).

Sticky cards were returned to the lab, where we counted numbers of common predatory insect families and individual coccinellid species. All coccinellids were identified to species except for those in the genera *Hyperaspis* (Chevrolat in Dejean) and *Brachiacantha* (Chevrolat in Dejean), which were identified to genus. Taxa counted at the family level included Dolichopodidae (Diptera), Anthocoridae (Hemiptera), Syrphidae (Diptera) and Chrysopidae (Neuroptera). Importantly, sticky cards are not efficient at capturing all natural enemies (Schmidt et al., 2008). Consequently, our inferences are limited to taxa that are readily captured by this technique.

2.2. Characterizing landscape composition

We used the 2009 Cropland Data Layer to characterize the area of major annual and perennial habitats within a 2 km radius of each study site (CDL, 56 m resolution) (USDA, 2010). Past research in the region found landscape variables at the 2 km scale to be

most predictive of coccinellid abundance (Gardiner et al., 2009b). We reclassified the CDL into three landcover types prior to analysis. A "forest" class contained deciduous, mixed, and coniferous forests in addition to woody wetlands, but was dominated by deciduous forest (73% of total class area). An "herbaceous perennial" class contained alfalfa, pasture, hayfields, grasslands and shrublands, and was dominated by hayfields and pasture (83%). Finally, an annual crop class contained annual field and vegetable crops and was dominated by corn and soybean (87%). These represent major classes of cover types that could be affected by expanding biofuel production and covered 85% of the study landscapes. Other habitats (barren, urban, open water, wetlands, orchards and vineyards) covered <15% of the study area and were not included in analyses. After reclassification, we used ArcGIS 9.3 to create 2 km buffers around the center of each sampled area (ESRI, 2008). The "isectpolyrst" tool of the Geospatial Modelling Environment (Beyer, 2010) was then used to calculate the proportion of the landscape composed of each cover class for the area falling within each buffer.

2.3. Coccinellid assemblages

2.3.1. Analysis of species composition

We compared the composition of coccinellid assemblages in corn, switchgrass and prairie habitats using multivariate analyses conducted in Primer vs. 6 (Clarke and Gorley, 2006). Abundance data were ln (x + 1)-transformed prior to analysis to downweight the influence of dominant species (Clarke and Gorley, 2006). Dissimilarity between sites was then quantified using the zero-adjusted, Bray–Curtis coefficient (Clarke et al., 2006), which alleviates multivariate heteroskedasticity when there are many zeroes. This metric describes two sites as maximally similar when they share the same species in the same relative abundances, and maximally dissimilar when they have no species in common. These differences were visualized by ordinating sites using non-metric multidimensional scaling (Clarke and Gorley, 2006). Statistical significance was assessed via pairwise comparisons between habitats (corn, switchgrass and prairie) obtained in an Analysis of Similarities ("ANOSIM") (Clarke and Gorley, 2006). An ANOSIM can detect differences in both the average composition and variability of assemblages between treatments. However, a permutational test for differences in multivariate dispersion (PERMDISP module for dispersion about the median in PRIMER) suggested variability in assemblages did not vary between treatments (P = 0.35). Consequently, any differences were due to changes in composition. Finally, the percent contribution of each species to community differences was quantified using the "SIMPER" module of Primer (Clarke and Gorley, 2006). Note, SIMPER only accepts the standard Bray–Curtis coefficient. While this metric is slightly different than the adjusted one used in the ANOSIM, dissimilarities using this metric were correlated to the adjusted coefficient (RELATE test of PRIMER for correspondence between two dissimilarity matrices: Spearman's ρ = 0.82, P = 0.001) and allowed us to use the SIMPER module, which provides an intuitive characterization of the species driving multivariate differences (Clarke and Gorley, 2006).

2.3.2. Species richness and abundance

We examined the relative importance of biofuel crop type, landscape composition, and their interactions as predictors of coccinellid species richness and captures of exotic and uncommon, native ladybeetles (see section on modeling approach below). To estimate species richness, we used EstimateS (Colwell, 2009) to calculate a Chao2 estimator of species richness for each site (Chao, 1984, 1987), with singletons and doubletons defined as species that occurred on only one or two sticky cards, respectively. Note, an anal-

ysis using rarefaction-based estimates of richness produced identical results, suggesting there was no difference in analyses using extrapolated (i.e., Chao 2) and rarefied richness. For this analysis, the genera Hyperaspis and Brachiacantha each contributed to richness estimates as single species. These genera contain multiple species; consequently, our estimates of species richness may be biased downwards. For analysis of abundance, we distinguished between exotic and uncommon (Table 1), native coccinellids because these taxa are functionally different (Giorgi et al., 2009) and because uncommon native coccinellids are of conservation concern (Harmon et al., 2006). Uncommon native taxa were defined to include all native species except Coleomegilla maculata (De Geer), which is the only abundant native in crop fields in our study area (Gardiner et al., 2009b, 2010; Losey et al., 2011). C. maculata also has a unique biology, feeding heavily on pollen (Lundgren and Wiedenmann, 2004), and is known to respond differently to biofuel crop type compared to other natives (Gardiner et al., 2010). Abundances were averaged across all traps for each site. Mean captures of exotics were ln-transformed prior to analysis.

2.3.3. Modeling species richness and abundance

We examined the relative importance of biofuel crop type, landscape composition, and their interactions as predictors of coccinellid species richness and abundances of exotic and uncommon, native ladybeetles. These three response variables (coccinellid richness, abundance of exotics, abundance of uncommon natives) were related to predictors that included: a categorical variable distinguishing between corn, switchgrass and prairie habitats ("H"), landscape variables describing variation in the area of annual crops ("L_{an}"), herbaceous perennials ("L_{hp}") and forest ("L_{fo}"), and two-way interactions between habitat and each landscape variable. We also included a "state" effect ("S," Wisconsin vs. Michigan) as a blocking variable to account for other potential sources of variability associated with each state (e.g., biological and/or sampling differences).

We used a model-selection approach to quantify evidence for 18 models predicting coccinellid richness and abundance of exotics and uncommon natives as a function of different combinations of habitat and landscape variables (Burnham and Anderson, 2002). The set included models predicting captures as a function of habitat alone (model 2, Tables 2 and 3), as a function of landscape composition (models 3–7), and as additive (8–12) or interactive (13–17) combinations of habitat type and landscape composition (Tables 2 and 3). We also included models with only an intercept (model 1) and an intercept plus a blocking effect of state (model 2) as null models. We calculated AIC$_c$-values for each model (Burnham and Anderson, 2002). These were used to derive ΔAIC$_c$ values and model weights, w, which were used to compare the strength of evidence for different models (Burnham and Anderson, 2002). Model weights approximate the likelihood that a given model will be the best in the set in repeated runs of an experiment. Models with ΔAIC$_c$ < 2 are considered to be strongly supported by the data, and are termed competing models (Burnham and Anderson, 2002). We used the most parsimonious (fewest variables) competing model for inference; these models contained a subset of the variables present in other competing models with little sacrifice of predictive power (Tables 2 and 3). To complement these statistics, we calculated a generalized coefficient of determination to quantify the amount of variation explained by each model (Nagelkerke, 1991).

We fit linear and generalized linear models as appropriate. For coccinellid diversity, we fit generalized linear models assuming a Poisson distribution using the "glm" function of R version 2.11.1 (Venables and Smith, 2010); this distribution was appropriate as species richness is a discrete variable. For exotic ladybeetle

Table 1
Coccinellids and four other families of predatory arthropods were captured with sticky cards in corn, switchgrass and prairie sites ($n = 60$) in southern Michigan and Wisconsin; data are mean and maximum captures per sticky card, total captures, percent of total catch, and designation of coccinellids as exotics ("EX"), common ("CN") or uncommon natives ("UN").

Taxon	$\bar{X} \pm SE$	Max	Total	%	Designation[a]
Coccinellid species					
Coccinella septempunctata L.	0.371 ± 0.022	10	706	5.93	EX
Coleomegilla maculata De Geer	0.222 ± 0.020	11	422	3.54	CN
Harmonia axyridis Pallas	0.170 ± 0.012	5	324	2.72	EX
Propylaea quatuordecimpunctata L.	0.158 ± 0.016	8	301	2.53	EX
Brachiacantha spp. Chevrolat in Dejean[b]	0.140 ± 0.016	15	267	2.24	UN
Cycloneda munda Say	0.035 ± 0.005	3	66	0.55	UN
Hippodamia variegata Goeze	0.019 ± 0.003	2	36	0.30	EX
Hippodamia parenthesis Say	0.015 ± 0.003	2	29	0.24	UN
Psyllobora vigintimaculata Say	0.006 ± 0.002	1	11	0.09	UN
Hyperaspis spp. Chevrolat in Dejean[c]	0.004 ± 0.001	1	7	0.06	UN
Hippodamia tredecimpunctata L.	0.003 ± 0.001	1	6	0.05	UN
Hippodamia convergens Guérin-Méneville	0.003 ± 0.001	1	5	0.04	UN
Coccinella trifasciata L.	0.001 ± 0.001	1	1	0.01	UN
Total Coccinellidae	1.147 ± 0.044	18	2181	18.32	
Other predator families					
Dolichopodidae	2.500 ± 0.127	114	4755	39.95	
Syrphidae	2.456 ± 0.089	35	4671	39.24	
Anthocoridae	0.095 ± 0.011	7	181	1.52	
Chrysopidae	0.060 ± 0.007	5	115	0.97	
Total other families	5.111 ± 0.157	116	9722	81.68	

[a] Uncommon native coccinellids were considered to compose <13% of total captures, which excluded *C. maculata* from this category.

[b] Composed of unknown proportion of two species: *Briachiacantha ursina* Fab. and *Brachiacantha albifrons* Say.

[c] Composed of one *Hyperaspis binotata* Say and six specimens in poor condition not identifiable to species.

Table 2
Model selection statistics for $i = 18$ models predicting coccinellid species richness and relative abundances of exotic and uncommon, native Coccinellidae as a function of habitat type (H), landscape composition (L_{an}, L_{fo}, L_{hp}), or additive or interactive combinations of habitat type and landscape variables; for each response variable, model selection statistics for competing models ($\Delta AIC_c \leqslant 2$) are bolded.

i	Predictor variables[d]	Cocc. richness[a]			Exotic cocc.[b]			Uncommon native cocc.[c]		
		ΔAIC_c	w_i	r^2	ΔAIC_c	w_i	r^2	ΔAIC_c	w_i	r^2
0	Intercept only	**0.1**	**0.24**	**0.00**	17.3	0.00	0.00	25.6	0.00	0.00
1	S	**0.0**	**0.26**	**0.04**	4.6	0.04	0.22	27.4	0.00	0.01
2	S + H	3.5	0.04	0.05	5.3	0.03	0.27	8.3	0.01	0.33
3	S + L_{an}	**1.8**	**0.10**	**0.04**	6.9	0.01	0.22	11.2	0.00	0.27
4	S + L_{fo}	2.2	0.09	0.04	6.7	0.01	0.22	25.2	0.00	0.08
5	S + L_{hp}	**1.9**	**0.10**	**0.04**	**0.0**	**0.38**	**0.30**	26.9	0.00	0.05
6	S + L_{an} + L_{hp}	4.0	0.03	0.05	**1.9**	**0.15**	**0.31**	10.4	0.00	0.31
7	S + L_{fo} + L_{hp}	4.2	0.03	0.04	**2.0**	**0.14**	**0.31**	24.8	0.00	0.12
8	S + H + L_{an}	5.3	0.02	0.06	7.4	0.01	0.28	**0.0**	**0.54**	**0.44**
9	S + H + L_{fo}	5.9	0.01	0.05	7.6	0.01	0.27	9.7	0.00	0.34
10	S + H + L_{hp}	5.3	0.02	0.06	2.4	0.11	0.33	9.5	0.00	0.35
11	S + H + L_{an} + L_{hp}	7.4	0.01	0.07	4.2	0.05	0.34	**1.1**	**0.31**	**0.46**
12	S + H + L_{fo} + L_{hp}	7.8	0.01	0.06	4.5	0.04	0.34	11.0	0.00	0.36
13	S + H + L_{an} + $H \times L_{an}$	10.2	0.00	0.06	10.0	0.00	0.31	3.2	0.11	0.46
14	S + H + L_{fo} + $H \times L_{fo}$	4.5	0.03	0.15	8.6	0.01	0.32	10.9	0.00	0.39
15	S + H + L_{hp} + $H \times L_{hp}$	6.1	0.01	0.13	6.8	0.01	0.34	13.1	0.00	0.36
16	S + H + L_{an} + L_{hp} + $H \times L_{an}$ + $H \times L_{hp}$	13.6	0.00	0.14	11.9	0.00	0.38	8.3	0.01	0.49
17	S + H + L_{fo} + L_{hp} + $H \times L_{fo}$ + $H \times L_{hp}$	9.8	0.00	0.19	8.5	0.01	0.42	17.7	0.00	0.41

[a] Statistics are from model predicting Chao 2 estimates of coccinellid species richness (Chao, 1984, 1987).

[b] Statistics are from model predicting the relative abundance of exotic coccinellids.

[c] Statistics are from model predicting uncommon native coccinellids (all native species excluding *Coleomegilla maculata*).

[d] Predictors are a categorical variable indicating whether a sample site was corn, switchgrass, or prairie habitat (H) and the proportion of annual crop (L_{an}), forest (L_{fo}) and herbaceous perennial habitat (L_{hp}) in the landscape within 2 km of sites. All models except the intercept-only model contain a blocking variable (S) to account for overall differences in captures between states.

abundance, we fit normal, linear models with the "lm" function of *R* (Venables and Smith, 2010). For uncommon natives, data contained many zeroes and were overdispersed, which was not ameliorated by data transformation. Consequently, a generalized, linear model with a negative binomial distribution was used for analysis of their abundance, implemented using the "glm.nb" function of the "MASS" package of *R* (Venables and Ripley, 2002). Using this, we modeled the total, summed catch of uncommon natives, including the number of traps as an offset to account for differences in sampling effort between states (Zuur et al., 2009).

AIC-based model selection statistics were then calculated using likelihood values output from these models.

2.4. Family-level abundances

We examined the impact of crop type and landscape composition on captures of dolichopodids, anthocorids, syrphids and chrysopids. Data were averaged across the entire season for each site to obtain the average number of each family captured per trap. Abundances of dolichopodids and syrphids were ln-transformed prior to analysis,

Table 3
Model selection statistics for i = 18 models predicting relative abundances of four predatory insect families as a function of habitat type (H), landscape composition (L_{an}, L_{fo}, L_{hp}), or additive or interactive combinations of habitat type and landscape variables; for each family, model selection statistics for competing models ($\Delta AIC_c \leqslant 2$) are bolded.

i	Predictor variables[a]	Dolichopodidae			Anthocoridae			Syrphidae			Chrysopidae		
		ΔAIC_c	w_i	r^2	ΔAIC_c	w_i	r^2	ΔAIC_c	w_i	r^2	ΔAIC_c	w_i	r^2
0	Intercept only	40.0	0.00	0.00	52.4	0.00	0.00	11.8	0.00	0.00	9.0	0.00	0.00
1	S	38.5	0.00	0.06	35.8	0.00	0.27	14.1	0.00	0.00	**1.9**	**0.11**	**0.14**
2	$S + H$	**0.3**	**0.16**	**0.54**	17.9	0.00	0.50	2.1	0.09	0.25	3.1	0.06	0.19
3	$S + L_{an}$	32.6	0.00	0.18	38.1	0.00	0.27	15.9	0.00	0.01	3.9	0.04	0.15
4	$S + L_{fo}$	37.0	0.00	0.12	38.1	0.00	0.27	16.3	0.00	0.01	3.2	0.06	0.16
5	$S + L_{hp}$	33.7	0.00	0.16	37.9	0.00	0.27	16.6	0.00	0.00	3.6	0.05	0.15
6	$S + L_{an} + L_{hp}$	29.4	0.00	0.25	40.3	0.00	0.27	18.5	0.00	0.01	5.6	0.02	0.16
7	$S + L_{fo} + L_{hp}$	31.0	0.00	0.23	40.3	0.00	0.27	18.9	0.00	0.01	5.1	0.02	0.16
8	$S + H + L_{an}$	**0.0**	**0.18**	**0.56**	16.8	0.00	0.53	4.7	0.02	0.25	4.4	0.03	0.21
9	$S + H + L_{fo}$	**0.3**	**0.16**	**0.56**	20.1	0.00	0.50	4.4	0.03	0.25	3.7	0.05	0.22
10	$S + H + L_{hp}$	**0.7**	**0.13**	**0.56**	15.5	0.00	0.54	4.8	0.02	0.25	5.4	0.02	0.19
11	$S + H + L_{an} + L_{hp}$	**0.8**	**0.12**	**0.57**	14.9	0.00	0.56	7.5	0.01	0.25	6.7	0.01	0.21
12	$S + H + L_{fo} + L_{hp}$	**0.1**	**0.18**	**0.58**	17.4	0.00	0.54	7.1	0.01	0.25	6.2	0.01	0.22
13	$S + H + L_{an} + H \times L_{an}$	3.5	0.03	0.57	15.3	0.00	0.58	**1.3**	**0.14**	**0.36**	**0.0**	**0.29**	**0.33**
14	$S + H + L_{fo} + H \times L_{fo}$	4.2	0.02	0.57	23.7	0.00	0.51	7.7	0.01	0.28	**0.5**	**0.22**	**0.32**
15	$S + H + L_{hp} + H \times L_{hp}$	5.6	0.01	0.56	**1.3**	**0.29**	**0.67**	**0.2**	**0.23**	**0.37**	10.4	0.00	0.20
16	$S + H + L_{an} + L_{hp} + H \times L_{an} + H \times L_{hp}$	10.1	0.00	0.59	**0.0**	**0.56**	**0.72**	**0.7**	**0.18**	**0.45**	8.0	0.01	0.33
17	$S + H + L_{fo} + L_{hp} + H \times L_{fo} + H \times L_{hp}$	9.1	0.00	0.59	2.8	0.14	0.70	**0.0**	**0.26**	**0.46**	8.6	0.00	0.33

[a] Predictors are a categorical variable indicating whether a sample site was corn, switchgrass, or prairie habitat (H) and the proportion of annual crop (L_{an}), forest (L_{fo}) and herbaceous perennial habitat (L_{hp}) in the landscape within 2 km of sites. All models except the intercept-only model contain a blocking variable (S) to account for overall differences in captures between states.

while anthocorid and chrysopid captures were square-root transformed. For analysis, we used the same modeling approach as for coccinellid richness and abundance of exotics and uncommon natives. Models were fit using multiple regression with the "lm" function of R vs. 2.11.1 for all families except syrphids (Venables and Smith, 2010). For syrphids, a variogram of residuals suggested there was spatial autocorrelation. To account for this, we used the "gls" function of the "nlme" package of R to fit an exponential spatial covariance structure (Zuur et al., 2009; Pinheiro et al., 2010), providing a significant improvement in model fit ($\chi^2 = 8.73$, df = 2, $P = 0.01$; test is for best saturated model, i.e., model 17 in Table 3, with and without spatial structure). For model selection, we fit this spatial model to syrphid abundance using maximum likelihood. Before inference, we re-parameterized the best model with restricted maximum likelihood as suggested by Wolfinger (1993).

3. Results

3.1. Coccinellid assemblages

Overall, 2181 coccinellids were captured on sticky cards, with 80% of the catch composed of three common exotic and one native species (Table 1). Coccinellid assemblages significantly differed between grasslands and corn (corn vs. switchgrass: ANOSIM $R = 0.53$, $P = 0.001$; corn vs. prairie: $R = 0.43$, $P = 0.001$), but were similar in switchgrass and prairie ($R = 0.00$, $P = 0.38$; Fig. 2A). The majority of the difference (80% of total dissimilarity) between habitats was due to an increased abundance of *C. maculata* in corn, *C. septempunctata* and *Brachiacantha* spp. in grasslands, and *H. axyridis* in corn (Fig. 2B).

There was little evidence that any models explained significant variation in coccinellid species richness ($0.04 \leqslant R^2 \leqslant 0.19$; Table 2). In contrast, data show that exotic and uncommon, native coccinellids were abundant in different habitats and landscapes. For exotics, all competing models suggest that relative abundance was negatively related to the area of herbaceous perennials in the landscape (Table 2, models 5–7; hereafter the ith model is referred to with only its number, e.g., model 5 is $i = 5$). Of these, the most parsimonious model ($i = 5$) predicted a twofold decline in exotic abundance with increases in the area of herbaceous perennials in the landscape (Fig. 3A, Online Supplementary Table 1). For uncommon natives, the best and most parsimonious model ($i = 8$) predicted greater abundance in switchgrass and prairie and a decline in captures to almost zero in landscapes composed of greater than 60% annual crops (Fig. 3B).

3.2. Family-level abundances

Habitat type affected three of four families, either directly or by modifying relationships between abundance and landscape composition. Data indicated that habitat type strongly affected captures of dolichopodids: all six competing models ($i = 2$, 8–12) contained a main effect of habitat type (Table 3), while five models ($i = 8$–12) contained an additional main effect of landscape composition. However, adding landscape variables yielded only small increases in predictive power compared to the simplest model ($i = 2$), which predicted captures only as a function of habitat (Table 3). This latter model predicted that dolichopodid captures were fourfold greater in switchgrass ($\bar{X}$ = 2.4 per trap, 95% Confidence Interval: 1.8, 3.4) and prairie ($\bar{X}$ = 2.3, 95% CI: 1.7, 3.2) compared to corn ($\bar{X}$ = 0.5, 95% CI: 0.4, 0.7; Online Supplementary Table 2).

Captures of anthocorids and syrphids were affected by landscape composition differently in corn compared to perennial grasslands (Fig. 4). All competing models explained captures of these taxa as interactive combinations of habitat type and landscape composition (Table 3). For anthocorids, both competing models ($i = 15$–16) contained an interaction between habitat type and the area of herbaceous, perennial habitat in the landscape (Table 3). The simplest of these models ($i = 15$) contained three fewer parameters than the best model with little sacrifice in predictive power (Table 3). This model predicted a strong increase in anthocorid captures in corn as the area of herbaceous perennials increased in the landscape (Fig. 4A), while it predicted that captures in grasslands were largely unaffected by landscape composition. Consequently, anthocorid captures were greater in corn compared to grasslands in landscapes with large areas of herbaceous, perennial habitat (Fig. 4A). For syrphids, three of four competing models ($i = 15$–17) contained an interaction between habitat type and the area of herbaceous perennials in the landscape (Table 3). Of these, the simplest model ($i = 15$) predicted a fourfold increase in syrphid
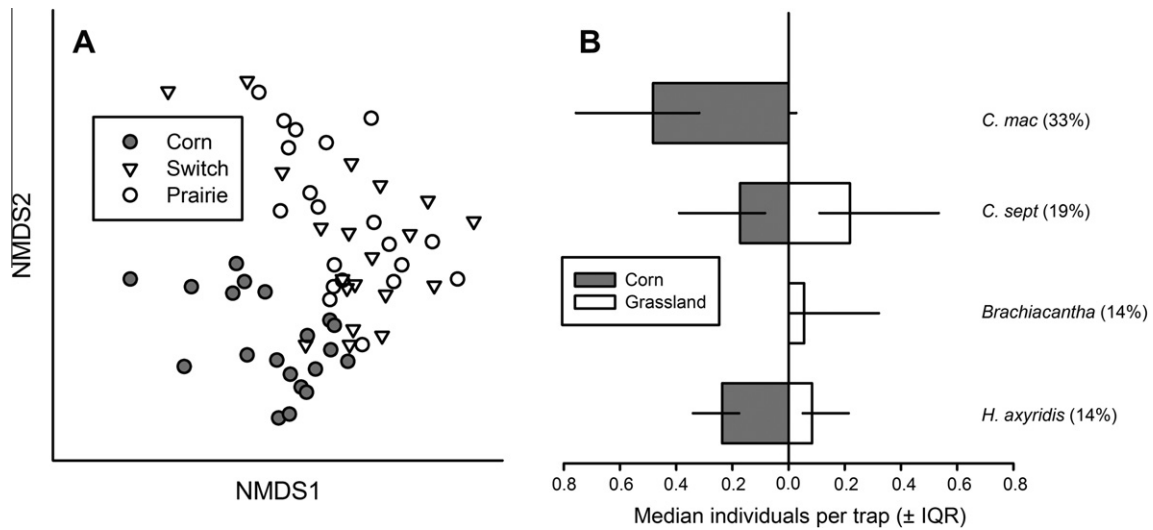
Fig. 2. (A) An ordination of Coccinellidae communities using non-metric multidimensional scaling (NMDS) shows their composition varied between corn and the two grassland crops (switchgrass and prairie; stress = 0.12). Each symbol represents a site; sites closer together in ordination space have similar species composition, as quantified by Bray–Curtis dissimilarities. (B) Sticky card captures (median ± interquartile range) of *Coleomegilla maculata* (*C. mac.*), *Coccinella septempunctata* (*C. sept.*), *Brachiacantha* sp., and *Harmonia axyridis* in corn and grassland (prairie and switchgrass sites combined). Percent contributions of species to dissimilarity between grassland and corn are in parentheses (Clarke and Gorley, 2006).
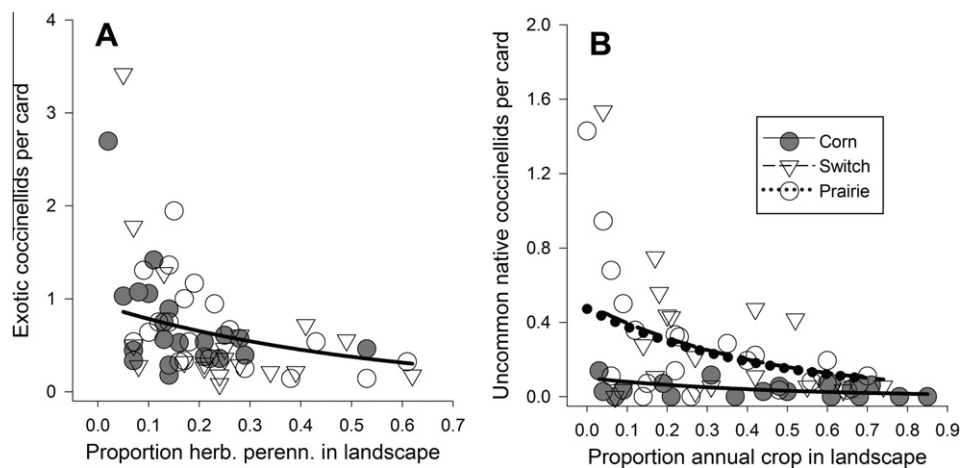
Fig. 3. (A) Mean sticky-card captures of exotic coccinellids decreased with the proportion of herbaceous, perennial habitats (herb. perenn.) in the surrounding 2 km, while (B) captures of uncommon, native coccinellids (species comprising <13% of total trap catch) were greater in switchgrass and prairie and decreased with the proportion of annual crops in the surrounding 2 km. Regression lines show back-transformed predictions of the most parsimonious, competing models ($\Delta AIC_c \leqslant 2$). The most parsimonious model for (A) fit a common regression line (solid line) for all crops, while different lines were fit for each crop in (B), as indicated in the legend. For clarity, regression lines are only shown for Michigan; lines for different states had identical slopes but different intercepts (Online Supplementary Table 1).

captures in corn as the area of herbaceous perennials increased in the landscape, with little change occurring in grasslands (Fig. 4B). In contrast to other families, there was little evidence that adding habitat or landscape variables improved prediction of chrysopid abundance: the null model ($i = 1$) was competitive and only contained an effect of state (Table 3 and Online Supplementary Table 2).

4. Discussion

Production of different biofuel crops could change the abundance of key natural enemies in agricultural landscapes at both local and landscape scales. Past work has shown that the abundance of different natural enemies varies between patches of different biofuel habitats (Gardiner et al., 2010). Here, we build on this work to show (1) these effects could occur at scales ranging from individual patches to entire mosaic landscapes and (2) that differ-

ent biofuel crops will change landscapes differently for different natural enemies. At local scales, dolichopodids and uncommon, native coccinellids were more abundant in switchgrass and prairie compared to corn, while the coccinellids *C. maculata* and *H. axyridis* were captured more frequently in corn (Figs. 2B and 3B). At broader scales, data suggest that shifting annual cropland to grasslands could negatively affect exotic coccinellids (Fig. 3A) or positively (Fig. 3B and Fig. 4) affect anthocorids, syrphids and uncommon, native coccinellids. These differential responses indicate that landscapes containing a mix of annual and grassland biofuel crops could provide habitat for a greater range of natural enemies than those composed of any one type of biofuel crop. Importantly, grassland sites were not managed for biomass, and switchgrass sites were not true monocultures (Werling et al., 2011); examining the impact of management on the conservation value of biofuel grasslands remains an important focus for future research.

Corn and grassland habitats may provide qualitatively different resources for natural enemies, leading to corresponding differences
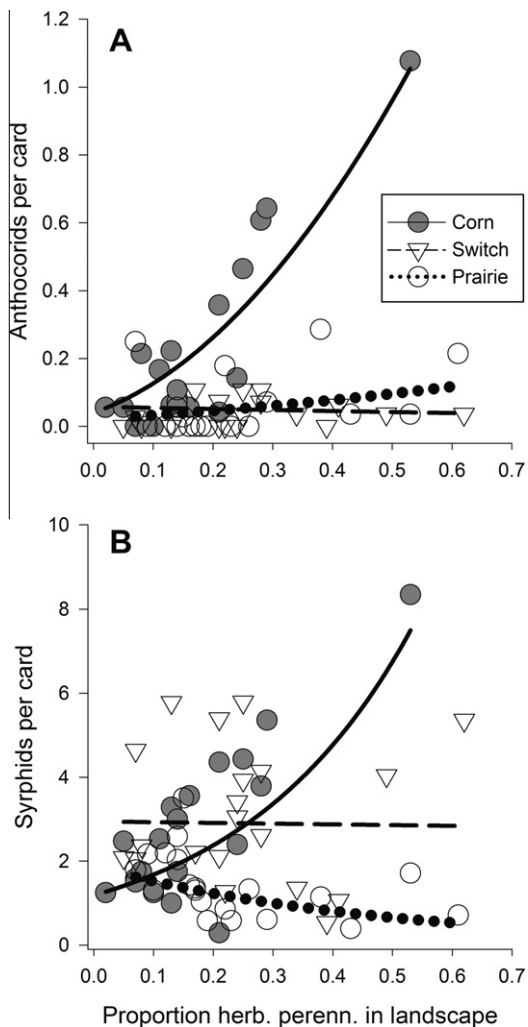
Fig. 4. Mean sticky-card captures of (A) Anthocoridae and (B) Syrphidae increased with the proportion of herbaceous, perennial habitats (herb. perenn.) in the landscape surrounding corn, but not switchgrass and prairie, sites. Landscape composition was measured for a 2 km radius around each site. Regression lines show back-transformed predictions of the most parsimonious, competing model ($\Delta AIC_c \leqslant 2$) for anthocorids and syrphids. For clarity, regression lines are only shown for Wisconsin in (A) and Michigan in (B). Lines for different states had identical slopes but different intercepts (Online Supplementary Table 2).

in the types of natural enemies that are abundant in these habitats. For example, corn sheds copious pollen that is fed on by *C. maculata* and hosts corn leaf aphid *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae), which may support increases in *H. axyridis* reproduction (Lundgren et al., 2004; Wright and Laing, 1980). These resources could have increased reproduction of these coccinellids in corn compared to the grasslands we sampled. In contrast to corn, biofuel grasslands may contain "novel" taxa whose resource requirements are relatively unique or unknown. For example, *Briachiacantha ursina* was among the *Brachiacantha* spp. that were more abundant in grasslands (Fig. 2) and feeds on coccids (Hemiptera) and aphids in ant nests as a larva (Smith, 1886; Wheeler, 1911). However, information on the diet of this coccinellid is based on limited observations that are a century old. Similarly, dolichopodids were abundant in grasslands and are known to be predators (Ulrich, 2004), but have received little attention as biological control agents. This highlights that novel biofuel crops may contain relatively under-studied natural enemies whose life histories and impacts will have to be elucidated by future research.

Data point to the potential for biofuel crops to have effects on natural enemies that extend beyond their borders to existing food crops. We found that the abundance of syrphids and anthocorids in corn increased with the area of herbaceous, perennial habitats in the surrounding landscape (Fig. 4). Both syrphids and anthocorids use floral resources as adults (Kevan and Baker, 1983; Kiman and Yeargan, 1985), while anthocorids feed directly on plant tissues and may prefer weeds as oviposition sites compared to crop plants (Lattin, 1999; Lundgren et al., 2009). Grasslands may provide them with these resources, increasing their overall abundance and the number of individuals moving into surrounding crops. We also found evidence for impacts in the opposite direction: exotic coccinellids declined in corn, switchgrass and prairie sites surrounded by grasslands (Fig. 3A), suggesting grasslands are less suitable than annual crops and forests for these natural enemies. This provides an interesting parallel to the work of Rand and Louda (2006), who showed that coccinellid abundance and predation of native aphids were elevated in grassland fragments surrounded by annual crops compared to those surrounded by other grassland. They hypothesized that annual crops provided resources that subsidized increased abundances of coccinellids which then moved into grasslands (Rand and Louda, 2006). Together with our work, this suggests that (1) there will be substantial opportunity for spillover of natural enemies between grassland biofuel crops and other crop habitats and (2) and that it can occur in both directions (from grasslands to annual crops and vice versa).

Biofuel crops could change landscapes to affect the relative abundance of exotic and uncommon, native coccinellids. Past research has suggested that exotic and native ladybeetles are associated with different landscape characteristics. In particular, Gardiner et al. (2009b) suggested that open landscapes with abundant grasslands favor native ladybeetles, while forested landscapes favor exotics. We found evidence that exotic coccinellids are less abundant in landscapes with grassland (Fig. 3A), while uncommon native coccinellid captures declined in landscapes composed of annual crops (Fig. 3B). Together with the work of Gardiner et al. (2009b), this suggests that native coccinellids will form a more dominant part of assemblages in open landscapes containing grasslands, either because exotic coccinellids favor wooded landscapes (Gardiner et al., 2009b) or are less abundant in open landscapes with herbaceous, perennial habitats (this study). More generally, these findings demonstrate that biofuel-driven changes in landscape composition could alter the landscape for exotic and native taxa (Fig. 3). In other words, the success of invasive species may depend on the composition of the landscapes they invade (With, 2002).

Biofuel crop production will change landscapes for natural enemies in taxon-specific ways and at different spatial scales. This suggests that no single biofuel crop is best-suited for all natural enemies at all scales, indicating it will be important to maintain landscapes with a diverse mix of biofuel crops. At local scales, such landscapes comprise a mosaic of patches that provide habitat for different types of natural enemies (Tscharntke et al., 2007). At broader scales, natural enemies may benefit from resources in one habitat (e.g., grasslands) and move into another to control pests (e.g., corn) (Tscharntke et al., 2005). Currently, perennial grasslands are less common in agriculturally-dominated landscapes than annual crops. For example, in our study region grasslands composed a median of 18% of the landscape (interquartile range: 13–26%), while corn and soybean occupied a median of 29% of the study area (interquartile range: 29–56%). Consequently, adding grasslands to these landscapes could support biofuel production, diversify farmscapes, and contribute to the conservation of natural enemies that find existing crop habitats unsuitable. Moreover, synthetic community attributes such as arthropod biomass and diversity have been shown to increase with the area of

perennial grasslands (Purtauf et al., 2005; Werling et al., 2011) and perennial, non-crop habitats in the landscape (Bianchi et al., 2006). This suggests that incorporating perennial biofuel crops into landscapes could provide community-wide benefits for natural enemies, despite the fact that individual taxa show idiosyncratic responses.

Importantly, the grassland habitats present in the study landscapes were not managed for biofuels but were used for grazing (i.e., pastures), for forage, or were unmanaged. The introduction of dedicated biofuel grasslands onto landscapes may produce effects on natural enemies that differ from those documented here, depending on the crops that are grown and how they are managed. Future work should aim to uncover the mechanisms underlying landscape-scale impacts like those documented here. Doing so will allow grassland biofuel crops to be managed to maintain resources – such as flowers or alternative prey – that could benefit natural enemies.

In summary, an increased demand for alternative fuels will drive changes in the composition of agricultural landscapes (Secchi and Babcock, 2007). These changes are expected to impact natural enemies that provide valuable pest control services (Landis and Werling, 2010; Werling et al., 2011). Understanding the impacts of landscape change on beneficial organisms at both a fine (habitat) scale and across larger mosaics could allow biofuel landscapes to be proactively designed to conserve valuable species and their services, produce food, and provide fuel (Gurr et al., 2003; Robertson et al., 2008; Webster et al., 2010).

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocontrol.2011.06.014.

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