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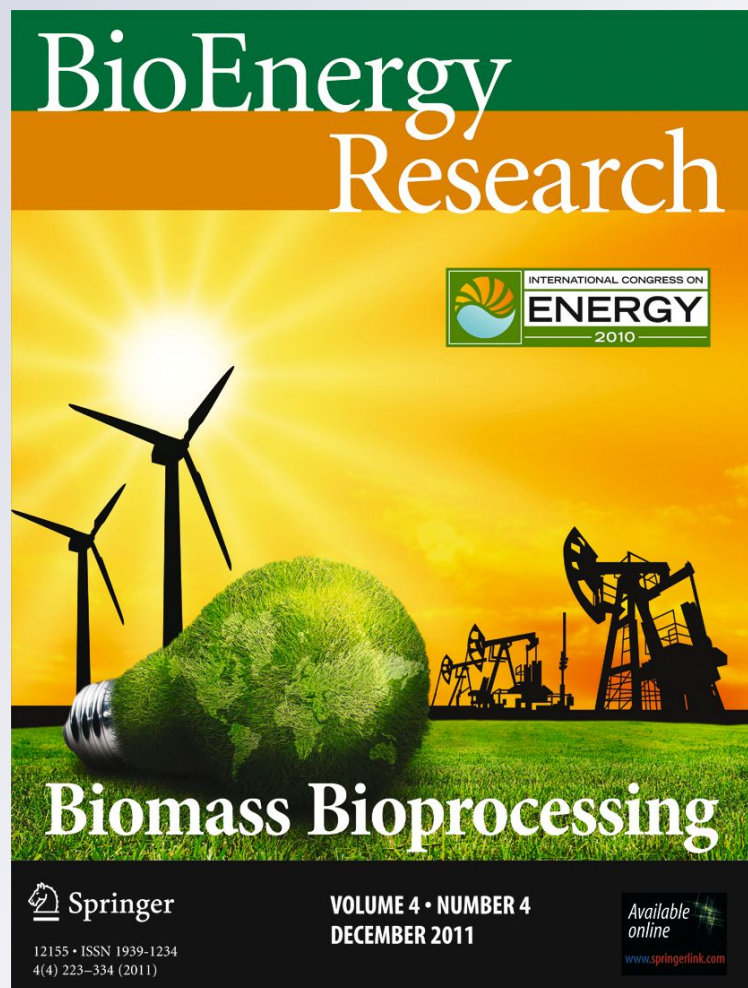
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# Agroenergy Crops Influence the Diversity, Biomass, and Guild Structure of Terrestrial Arthropod Communities

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**Abstract** Expanded production of contemporary bioenergy crops (e.g., corn) is considered a threat to the conservation of biodiversity, yet next-generation perennially based crops (switchgrass, mixed-grass–forb prairie) may represent an opportunity for enhancing biodiversity in agricultural landscapes. We employed a multi-scaled approach to investigate the relative importance of feedstock selection, forb content, patch size, and landscape-scale habitat structure and composition as factors shaping the diversity and abundance of terrestrial arthropod communities and the biomass of functional groups of arthropods associated with the provisioning of ecosystem services. Compared to intensively managed annual corn fields, switchgrass and mixed-grass–forb prairie plantings were associated with a 230% and 324% increase in arthropod family diversity and a 750% and 2,700% increase in arthropod biomass, respectively. Biomass of arthropod pollinators, herbivores, predators,

and parasites were similarly the highest in mixed-grass–forb prairie, intermediate in switchgrass plantings, and the lowest in cornfields. Community-wide biomass and that of several functional arthropod groups were positively linked to increasing forest cover and land cover diversity surrounding biomass plantings, while pollinator and detritivore biomass was lower in smaller fields. Results not only suggest that the choice of biomass feedstock will play an important role in shaping within-field arthropod diversity but also indicate an important role for the composition of this surrounding landscape. Collectively, our results suggest that selection of perennially based biomass feedstocks along with careful attention to crop placement have important potential to enhance biodiversity conservation and the provisioning of ecologically and economically important arthropod-mediated ecosystem services in future agricultural landscapes.

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## Introduction

The ecological sustainability of dedicated agriculturally based biomass crops (agroenergy) will depend on the ability of crops to support native biodiversity and sponsor important ecosystem services [1–3]. The historical focus on maximizing agricultural production without accounting for trade-offs with economically important ecosystem services [4] has resulted in degradation of water, soil quality, and biodiversity; increases in arthropod crop pests; and reductions in populations of pollinating insects [4–9]. Federal production mandates for next-generation, cellulosic biomass crops in the USA [10] are projected to impact over

100 million ha of land [11], particularly in the grassland biome [12] that has already sustained heavy biodiversity losses associated with conversion to agriculture [13]. These mandates provide the USA, in particular, with a unique opportunity to design new agroenergy production systems that incorporate biodiversity conservation and the delivery of ecosystem services into production goals [1, 14] with potential to impact large geographic regions. In this regard, there remains a critical need for empirical data capable of guiding the design implementation of these new agroenergy production systems [2, 3, 15, 16].

Arthropods are key mediators of ecosystem function in terrestrial systems. Any changes in the way that humans appropriate plant biomass for bioenergy production are likely to shape the functioning of agricultural landscapes. Herbivorous arthropods will act as pests of biomass crops, capable of reducing the quantity or quality of biomass harvested [17]. Conversely, other arthropod groups such as decomposers, pollinators, predators, and parasitoids will enhance nutrient mineralization and plant performance in biomass crops [18, 19], enhance pollination services [20], and assist in the control of herbivorous crop pests [17, 21], respectively. Inasmuch as expansion of biomass production can shape arthropod communities and influence arthropod biodiversity, selection of biomass crops can change the ways arthropod-mediated ecosystem services such as pollination and pest suppression are distributed in agricultural landscapes [14, 17].

Alternative biomass feedstocks may differ profoundly in their ability to support native biodiversity and provision ecosystem services [3, 20, 23–25]. In regard to terrestrial arthropod populations, low-input, high-diversity mixed-grass prairie reconstructions (sensu [26]) and switchgrass monocultures (*Panicum virgatum*) have recently been

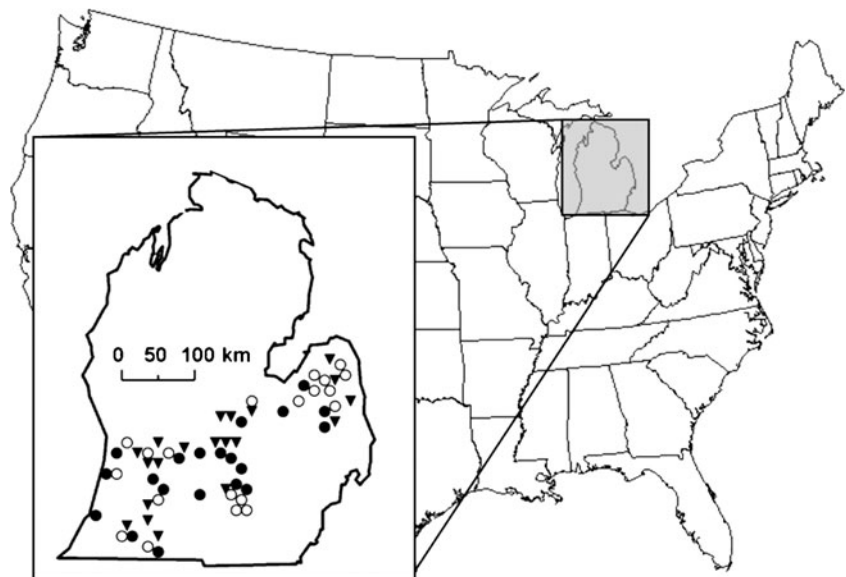
found to support a greater diversity and abundance of bees and a higher abundance of two important predator groups (Coccinellids and Dolichopodids) than corn [20]. Here, we take a community-wide perspective and build on previous work by examining the diversity, richness, and feeding guild structure of terrestrial arthropod communities in crops ranging from an intensively managed, annual monoculture to diverse plantings of perennial grasslands. We also examine the importance of other local and landscape-scale factors relevant to biomass production and known to shape terrestrial arthropod communities: (1) field size [20, 27], (2) landscape composition and diversity (reviewed in [5, 21, 23]), and (3) biofuel crop vegetation structure and composition [28, 29].

## Methods

### Study Design and Site Selection

Twenty sites of each of the three biomass planting treatments were selected from established fields throughout southern Michigan (Fig. 1). We visited 28 sites in 2008 (prairie=11, switch=9, corn=8) and 32 sites in 2009 (prairie=9, switch=11, corn=12). Because market demand for perennial biomass crops is low, these fields were not actively managed for biomass production, but primarily for wildlife habitat or as native community restorations. Consequently, switchgrass fields frequently contained a small forb component, including flowering plants, and so were not always strict monocultures. Within each treatment, we selected sites representing a range of crop stand structural heterogeneity from within landscapes varying as much as possible in the amount of non-crop habitat they

**Fig. 1** Map of the study region in the southern peninsula of Michigan, USA. Locations of the 20 mixed-grass–forb prairie (filled circles), 20 switchgrass (open circles), and 20 corn (triangles) study sites are indicated



contained. Because we wished to examine the importance of patch size in shaping arthropod communities, we also selected patches to vary as widely as possible in size (prairie 2–101 ha; switchgrass 2–42 ha; corn 3–65 ha). Biomass fields were located a minimum distance of 5 km from other sites.

#### Arthropod Richness, Biomass, and Functional Groups

Abundance is typically used as a response variable in the analysis of community structure along ecological gradients, but biomass is a better indicator of the functionality of species within a community and is strongly correlated with metabolism [30]. We sampled terrestrial arthropods via sweep net samples of aboveground vegetation near the geographic center of each field between (1) 22 May–20 June and (2) 16 June–4 July in both years of the study. Each of two within-patch sweep sample transects began at a distance of 50 m in opposite directions from the field center on a north–south axis. Each sample consisted of 50 sweeps taken while slowly moving toward the plot center. Both within-field samples were combined, sealed in plastic bags, and transferred to 90% ethanol solution for storage. We identified insects to the family level and placed families in functional groups (decomposers, fungivores, sap and wood feeders, herbivores, predators, parasites, and parasitoids (hereafter predators *sensu lato*), or “other” i.e. omnivores) according to Johnson and Triplehorn [31]. We also placed families whose members are known to be important pollinators in a separate category (Supplementary Material, Table S1). Spiders in the suborder Palaptores were not further identified to the family level. All functional group categories were mutually exclusive except for pollinators. We measured the length of each individual and estimated individual mass using published length–regression estimates [32, 33]. Combining samples from both sampling periods, we computed biomass at the patch level for the entire community and each functional group. Patch-scale estimates of arthropod family richness were obtained using the individual-based asymptotic richness estimator in package “vegan” [34] in R [35].

#### Within-Patch Habitat Structure

During the second site visit each season, we characterized the vegetation of plantings within a series of 50-m-long × 50-m-wide transects to determine how vegetation structure and within-field variation in that structure may affect the spatial distributions of arthropods. To obtain representative samples of fields differing in area while avoiding pseudo-replication, we surveyed a single transect in the smallest patches increasing transect number with patch size up to seven in the largest patches, then aggregated information at

the patch-scale prior to analysis. Transects were oriented and surveyed in linear series such that no transect began or ended closer than 50 m from a patch edge and one transect ran through the geographic center of the field encompassing the arthropod sampling area. We randomly selected five non-overlapping sampling points within each transect at which we recorded the canopy coverage of forbs. Forb coverage was estimated on the basis of non-overlapping percentages of forbs and grass using a Daubenmire quadrat viewed from 1.5 m directly above [36]. Cover estimates were assigned an index number corresponding to a range of vegetation coverage (1=0–5%, 2=5–25%, 3=25–50%, 4=50–75%, 5=75–95%, 6=95–100%). Mean values of canopy cover were computed at the patch scale.

#### Patch and Landscape Variables

Expansion of biomass production may alter ability of landscapes to sponsor ecosystem services [8, 17, 23] because changes in landscape composition and structure can affect important functional groups differently [37]. To address this, we derived landscape characteristics within a 1.5-km radius of each study site using the 2009 Cropland Data Layer (56 m resolution) [38]. We categorized patches as containing cropland (e.g., corn, soybeans), herbaceous perennial habitats (including grasslands), forest, and urban land (>60% impervious surface). We pooled all other land cover classes into a fifth category (<1% of total area) that were excluded from analyses. The accuracy of land-use categories was directly verified during site visits. The proportion of the landscape within 1.5 km of each site in these cover types was calculated using ArcGIS 9.3 [39]. We used the Patch Analyst 4.0 extension to ArcGIS to calculate a modified Simpson's Diversity Index [40].

#### Statistical Analysis

We used a multimodel inference approach to determine the relative importance of five environmental variables in explaining the following attributes of the terrestrial arthropod community in feedstock plantings: (1) community-wide family richness and (2) biomass, and the biomass of (3) detritivores, (4) fungivores, (5) pollinators, (6) omnivores, and (7) predators. The five explanatory variables included (1) an index of % ground cover in forbs, (2) biomass feedstock type, (3) patch size, (4) percentage of forest cover in the landscape, and (5) Simpson's index of land cover diversity (after [21]). Because species richness generally increases with patch size in an asymptotic and non-linear fashion [27], we log-transformed the patch size prior to analysis to linearize the species–area relationship.

Because arthropod community variables followed Poisson distributions typical of count data and were over-dispersed,

we modeled arthropod community variables using either negative-binomial or quasi-Poisson regression with a log link function [41]. Modeling began by entering all independent variables (Table 1) into a full generalized linear model. Next, all possible subsets of the full model were analyzed using the multimodel inference package, MuMin in R v. 2.11.1 [35]. We used this package to estimate model coefficients and bias-corrected quasi-Akaike's information criterion (QAIC<sub>c</sub>) values, an adaptation of AIC that accounts for potential overdispersion in count data and contains a small sample size adjustment [42]. Next, differences between the QAIC<sub>c</sub>-best model and the other candidate models ( $\Delta$ QAIC<sub>c</sub>) were used to calculate Akaike weights ( $\omega_i$ ) for each candidate. Weights of ranked models were then summed to construct a 90% confidence set of candidate models. Akaike weights were then recalculated for each model in the 90% confidence set and used to calculate model-averaged parameter estimates and summed variable weights for each variable in the global model. Finally, Akaike weights for classes of variables were summed to assess the relative importance of different characteristics of the study sites (Tables 3 and 4). A full discussion of the information-theoretic approach to model/variable selection used here can be found in Burnham and Anderson [42]. We tested for spatial autocorrelation among sites by computing Moran's I as a function of spatial distance using the R package [43]. Because correlograms of Moran's I at various distance lags and the resulting correlogram showed no evidence of spatial dependence among observations, we did not take into account any spatial autocovariate in the models.

**Results**

Crop Vegetation Structure, Patch Size, and Landscape Composition

The average ground cover in herbaceous forbs, the fraction of the landscape in forest, and the land cover diversity of surrounding landscapes did not differ among corn, prairie, and mixed-grass–forb prairie study sites (Table 1). Mean patch size of switchgrass study sites was significantly smaller than prairie or corn fields. Row crops, forest cover, and, to a lesser degree, herbaceous perennial habitat types dominated landscapes surrounding field sites (Table 2). Two sites were in landscapes dominated by urban land use.

Arthropod Community Composition and Biomass

We captured 20,765 arthropods from 143 families (mixed prairie=132; switchgrass=108; corn=60). The feedstock containing the most families not captured in another feedstocks type (unique families) was prairie (mixed prairie=27; switchgrass=8; corn=3, Supplementary Material, Table S1). Family richness, total arthropod biomass, and the biomass of all functional groups exhibited a pattern in which the highest biomass was associated with mixed-grass–forb prairie, the lowest biomass with corn fields, and intermediate levels with switchgrass plantings (Table 1).

Detritivore captures were dominated by scorpionflies (Panorpidae); fungivores by minute brown scavenger beetles (Latridiidae) and fungus beetles (Endomychidae);

**Table 1** Marginal mean values of habitat variables and metrics of the terrestrial arthropod community associated with corn (n=20), switchgrass (n=20), and mixed-grass–forb prairie (n=20) fields throughout southern Michigan

Variable	Corn (SE)	Switchgrass (SE)	Prairie (SE)	Critical value	P
<i>Habitat variables</i>					
Forb index (1–6)	1.38 (0.13)	1.43 (0.12)	1.67 (0.12)	$F_{2,57}=1.1$	0.34
Patch size (ha)	18.52 (3.63)a	6.41 (3.63)b	19.57 (3.63)a	$F_{2,57}=4.0$	0.02
% forest cover (1,500-m radius)	0.30 (0.05)	0.37 (0.05)	0.34 (0.05)	$F_{2,57}=0.6$	0.56
Simpson's D (0–1)	0.57 (.02)	0.60 (0.02)	0.60 (0.02)	$F_{2,57}=1.0$	0.38
<i>Arthropod community variable</i>					
Total family richness (# families/sample)	20.70 (1.02)a	67.2 (1.84)b	74.93 (1.55)c	$\chi^2_2=57.56$	<0.001
Total biomass (μg/sample)	1,044.50 (223.67)a	8,847.10 (1,978.38)b	29,485.40 (6,593.25)c	$\chi^2_2=27.31$	<0.001
Detritivore biomass (μg/sample)	73.24 (16.70)a	248.95 (388.62)a	1,705.10 (388.62)b	$\chi^2_2=32.99$	<0.001
Fungivore biomass (μg/sample)	74.90 (16.86)a	245.10 (54.92)b	978.00 (218.80)c	$\chi^2_2=27.00$	<0.001
Herbivore biomass (μg/sample)	222.20 (49.80)a	3,052.25 (682.62)b	9,082.20 (2,030.95)c	$\chi^2_2=26.75$	<0.001
Predators, parasites, and parasitoids (μg/sample)	531.60 (118.98)a	4,355.50 (974.03)b	9,939.60 (2,222.67)c	$\chi^2_2=22.75$	<0.001
Omnivore biomass (μg/sample)	46.30 (10.46)a	531.70 (119.00)b	6,027.90 (1,347.991)c	$\chi^2_2=36.16$	<0.001
Pollinator biomass (μg/sample)	20.00 (1.00)a	50.93 (6.82)b	64.94 (6.90)b	$\chi^2_2=29.53$	<0.001

Marginal mean values and critical and significance values are associated with general linear models (habitat variables) and QAIC<sub>c</sub>-best models for each functional group (Tables 3 and 4). Letters indicate significant (P<0.05) differences in mean values based on post hoc or likelihood ratio tests

**Table 2** Descriptive statistics of the percentage of land cover associated with different land-use types surrounding study sites in southern Michigan (1,500 m radius)

Land cover type	% of land cover surrounding site	
	Range	Mean (SD)
Row crop	0.01–0.82	0.33 (0.25)
Herbaceous perennial	0.00–0.49	0.12 (0.11)
Forest	0.01–0.75	0.34 (0.21)
Urban	0.00–0.67	0.06 (0.12)
Water	0.00–0.41	0.06 (0.09)
Other	0.00–0.21	0.05 (0.06)

omnivores by tumbling flower beetles (Mordellidae); and pollinators by honey bees (Apidae), metallic bees (Halictidae), and plasterer bees (Colletidae) (Supplementary Material, Figure S1).

### Arthropod Community Richness and Biomass

Family richness was primarily affected by biofuel crop type (Table 3). The QAIC<sub>c</sub>-best model ( $\hat{c}=7.12$ ) predicted a significant increase in biomass in perennial habitats compared with corn (switchgrass=230%; prairie=324%; Table 3). These effects received the highest possible support across the entire model set ( $\omega_+=1.00$ ) indicating this variable was consistently included in the most predictive models. Variable weights provided minimal support for predictors describing forb cover, patch size, forest cover, or land cover diversity ( $\omega_+\leq 0.50$ ; Table 3).

Community-wide biomass was affected by crop type, forest cover, and landscape diversity. The QAIC<sub>c</sub>-best model ( $\hat{c}=1.24$ ) predicted roughly 750% increase in biomass in switchgrass and a 2700% increase in biomass in prairie compared with corn (Table 3). Patches with a greater percentage of forest cover surrounding them and those in landscapes containing a greater diversity of land cover types had higher overall arthropod biomass forest cover surrounding patches. These effects were heavily supported (% forest cover:  $\omega_+=0.93$ ; Simpson's  $D$ :  $\omega_+=1.00$ ) compared to other predictors ( $\omega_+\leq 0.26$ ; Table 3).

### Arthropod Functional Group Biomass

The representation of arthropod functional groups was relatively conserved across crop types (Fig. 2), though herbivores were proportionally more represented in perennial feedstocks and predators were less represented in mixed-grass-forb prairie due to an increasing presence of omnivores. Communities were largely dominated by two functional groups: (1) herbivores and (2) predators.

Variation in detritivore biomass was best explained by crop type, patch size, and landscape diversity (Table 4). The QAIC<sub>c</sub>-best model ( $\hat{c}=11.1$ ) predicted higher detritivore biomass in smaller patches and more diverse landscapes. The model also indicated that prairie plantings had 2,300% more detritivore biomass than cornfields which were similar in biomass to switchgrass (Table 1). These three variables received very strong support ( $\omega_+=1.00$ ) across the entire model set compared to other variables ( $\omega_+\leq 0.49$ ; Table 4).

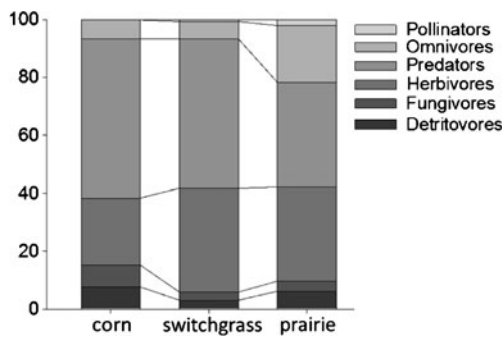
**Table 3** Parameter estimates ( $\beta\pm$ unconditional SE) from the QAIC<sub>c</sub>-best model predicting community-wide biomass and family richness in corn, switchgrass, and perennial grasslands

Parameter	Family richness		Total biomass	
	$\beta\pm$ SE	$\omega_+$	$\beta\pm$ SE	$\omega_+$
Intercept	3.03 (0.14)***		4.58 (0.79)***	
Crop <sup>a</sup>		1.00		1.00
Switchgrass	0.84 (0.16)***		2.05 (0.55)***	
Prairie	1.19 (0.18)***		3.36 (0.54)***	
Forb index		0.13		0.26
Log <sub>10</sub> (PSIZ) (ha)		0.50		0.20
% forest cover		0.44	1.16 (0.45)*	0.93
Simpson's $D$		0.33	2.66 (0.85)**	1.00

Variable weights ( $0\leq\omega_+\leq 1$ ) quantify relative support for each variable across the entire set of models, which contained all possible combinations of predictors. Variable weights obtained by summing  $\omega$  for all models in the set that included a given variable; weights approximate the likelihood a given variable will be included in the model in repeated runs of an experiment. Blank spaces indicate a parameter was not included in the QAIC<sub>c</sub>-best model

\* $0.01\leq P\leq 0.05$ ; \*\* $0.001\leq P\leq 0.01$ ; \*\*\* $P<0.001$  (significance codes for likelihood ratio  $\chi^2$ ; critical values)

<sup>a</sup> Corn was the reference category



**Fig. 2** Representation of terrestrial arthropod functional groups as a percentage of total biomass in three agroenergy feedstocks. Values refer to marginal mean values associated with QAIC<sub>c</sub>-best models (Table 2)

Biomass of herbivores was best explained by crop type, percentage of forest cover, and landscape diversity. The QAIC<sub>c</sub>-best model ( $\hat{c}=3.1$ ) predicted a roughly 1,300% increase in herbivore biomass in switchgrass compared to corn and a 2,900% increase in biomass in mixed-grass–forb prairie ( $\omega_+=1.00$ , Tables 1 and 3). Herbivore biomass increased with the percentage of forest cover and diversity of surrounding land cover types. Weighting for the support of these effects was very high ( $\omega_+=1.00$ ), compared to other predictors ( $\omega_+\leq 0.68$ ) indicating those variables were not consistently included in the most predictive models.

Predator biomass was also best explained by crop type and landscape diversity but was negatively related to patch size. The QAIC<sub>c</sub>-best model ( $\hat{c}=3.2$ ) indicated predator biomass to be 2,200% higher in switchgrass and 8,100% higher in mixed-grass–forb prairie than in corn fields (Tables 1 and 4). There was as significant effect of declining predator biomass in smaller patches and increas-

ing predator biomass in more diverse landscapes (Table 4). Crop type ( $\omega_+=1.00$ ), landscape diversity ( $\omega_+=1.00$ ), and patch size ( $\omega_+=0.82$ ) were weighted strongly, compared to other predictors ( $\omega_+\leq 0.38$ ). Predator biomass was correlated with herbivore biomass across crop types (Fig. 3). Sites with the most variation in their predator/herbivore biomass ratio were those with the highest herbivore biomass.

Pollinator biomass was affected primarily by biofuel crop type and a negative relationship with patch size (Table 4). The QAIC<sub>c</sub>-best model ( $\hat{c}=3.1$ ) predicted roughly a 280% increase in biomass in mixed-grass–forb prairie and switchgrass compared with corn. These effect received the highest possible support across the entire model set (both  $\omega_+=1.00$ ; Table 4) with remaining predictors exhibiting significantly lower weights ( $\omega_+\leq 0.72$ ). We did not examine habitat factors shaping the biomass of the omnivore or fungivore groups because the global models for these groups failed to converge.

**Discussion**

Accounting for how crop selection and placement will shape biodiversity in agricultural landscapes is critical to understanding the ecological and economic sustainability of next-generation agroenergy production systems [1, 3]. Our results not only point to crop selection as a consistently important factor in shaping arthropod diversity and biomass but also emphasize an important role for crop placement in determining the diversity and biomass of terrestrial arthropod communities and the provisioning of arthropod functional groups responsible for important ecosystem services.

**Table 4** Parameter estimates ( $\beta\pm$ unconditional SE) from the QAIC<sub>c</sub>-best model predicting the biomass of (1) detritivores, (2) herbivores, (3) predators, and (4) pollinators in corn, switchgrass, and perennial grasslands

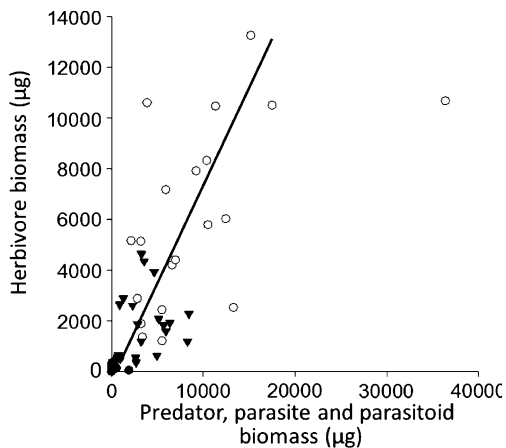
Parameter	Detritivore biomass		Herbivore biomass		Predator biomass		Pollinator biomass	
	$\beta\pm$ SE	$\omega_+$	$\beta\pm$ SE	$\omega_+$	$\beta\pm$ SE	$\omega_+$	$\beta\pm$ SE	$\omega_+$
Intercept	3.04 (2.01)*		6.52 (0.19)***		3.32 (0.69)***		1.66 (4.87)	
Crop <sup>a</sup>		1.00		1.00		1.00		1.00
Switchgrass	0.16 (0.89)		1.67 (0.33)***		2.62 (0.34)***		4.23 (4.86)*	
Prairie	3.05 (0.09)***		2.94 (0.31)***		3.31 (0.44)***		6.96 (4.83)*	
Forb index		0.49	0.24 (0.76)*	0.68		0.30		0.17
Log <sub>10</sub> (PSIZ) (ha)	-3.21 (1.09)**	1.00		0.19	0.64 (0.29)*	0.82	-1.72 (0.57)**	1.00
% forest cover		0.22	2.59 (0.44)***	1.00		0.38	1.70 (0.19)*	0.72
Simpson's <i>D</i>	5.17 (2.23)*	1.00	4.51 (0.78)***	1.00	2.84 (0.85)**	1.00		0.40

Following Table 2, variable weights ( $0\leq\omega_+\leq 1$ ) quantify the relative support for each variable across the entire set of models. Weights approximate the likelihood a given variable will be included in the model in repeated runs of an experiment. Blank spaces indicate a parameter was not included in the QAIC<sub>c</sub>-best model

\* $0.01\leq P\leq 0.05$ ; \*\*\* $P<0.001$ ; \*\* $0.001\leq P<0.01$  (significance codes for likelihood ratio  $\chi^2$  critical values)

<sup>a</sup> Corn was the reference category





**Fig. 3** Biomass of terrestrial arthropod herbivores vs. predators in corn (filled circles), switchgrass (triangles), and prairie (open circles) fields in southern Michigan. Herbivore biomass was important in explaining predator biomass, and there was no effect of crop type on the relationship (ANOVA: herbivore biomass  $F_{2,56}=20.2$ ,  $P<0.001$ , crop type  $F_{2,46}=0.9$ ,  $P=0.38$ ). These results suggest that the natural enemy community may be responding to the herbivore community in a numerical fashion

We found that the diversity and biomass of arthropod communities associated with two types of candidate perennial biomass plantings were substantially enhanced relative to those associated with corn ethanol production. Compared to intensively managed annually planted corn fields, switchgrass and mixed-grass–forb prairie plantings were associated with a 230% and 324% increase in arthropod family diversity and a 750% and 2,700% increase in arthropod biomass, respectively. Rather than focusing on the known positive relationship between plant and arthropod diversity [44, 45], we opted to define feedstock type based on the three categories of plantings most likely to first enter industrialized biomass production. In addition to plant diversity, per se, an important consideration in the development of perennial feedstock crops will be decisions about the inclusion of forb species in mixed-species polycultures. We found that the selection of categorically different planting types was more important than within-field forb cover in shaping the arthropod community metrics we measured, including the biomass of most major arthropod functional groups (but see [21]).

Local arthropod diversity is commonly greater within more heterogeneous landscapes [7, 46–48] and those with more forest cover [21]. We found that land cover diversity was unimportant compared to crop selection in explaining arthropod diversity but that landscape context was important in explaining community-wide arthropod biomass. Specifically, local biomass increased with surrounding forest cover and land cover diversity. Forest cover is strongly and negatively related to the land cover of row crops in this region and at these same study sites specifically [24, 25].

Together, these results indicate that the ability of arthropods to colonize biomass plantings is dependent upon the presence of source habitat in the surrounding landscape.

Herbivorous arthropods represented a major component of the arthropod community we sampled (Fig. 2) whose biomass increased 1,300% in switchgrass and 2,900% in mixed-grass–forb prairie relative to corn. Herbivore biomass was dominated by sucking insects with chewing herbivores being a minor component of overall biomass (Figure S1). Paralleling community-level responses, we found that herbivore biomass was enhanced in more diverse and forest-dominated landscapes. Herbivores are not known to directly control grass biomass in prairie systems but may control forb biomass and have important indirect effects [49], such as increasing litter quality and decomposition [50], contributing nutrients [51], and changing the through-fall chemistry [52] and energy demands [53] of damaged plants.

Previous studies investigating the role of predatory and parasitic arthropods in prairies have revealed a variety of controls on herbivorous arthropod populations through lethal and nonlethal effects that alter individual fitness and behavior [21, 49]. By affecting herbivorous arthropod populations, predatory arthropods can also increase primary production through top-down trophic cascades [54–56]. Perhaps not surprisingly, then, our results support the contention that the biomass of natural enemies may be responding to the herbivore community in a numerical fashion (Fig. 3). But while predator biomass was also positively related to forest cover, predator populations did not increase in more diverse landscapes and were, instead, reduced in larger patches. One possibility is that forested habitats act as important source populations for populations of some predators and parasites that have a limited ability to disperse into corn and perennial grassland habitats.

Declines in populations of native bees and other pollinators associated with agricultural intensification have caused reduced crop yields with associated drops in economic return to farmers [57, 58]. Results of this study found that arthropod pollinator biomass was strongly influenced by crop type, with mixed-grass–forb prairies having the greatest pollinator biomass with relatively little difference between switchgrass and corn fields. These crop-based biomass responses are consistent with those of Gardiner et al.'s [23] focal study on bees in this system and the impact of agricultural intensification on pollinators in general [59]. Yet, while those authors found that bee abundance increased with field size, we found that pollinator biomass declined with crop size. In this context, our results suggest that pollinator abundance may trade-off with functional biomass in response to patch size and that pollination services provided to both cellulosic and contemporary crops may be more dependent on the composi-

tion of the surrounding landscape than has previously been recognized [9].

Arthropod detritivores and scavengers directly and indirectly affect decomposition, carbon flux, biogeochemical cycling, and primary production [49, 60, 61], making them the dominant mediators of energy flow and nutrient cycling in many ecological systems. Dead arthropods themselves also contribute to detrital resources and represent significant pools of elements such as calcium [60] and a large number of detritivores feed heavily on fungi [61]. Detritivore biomass was dominated by scarab beetles and scorpionflies (Supplementary Material, Figure S1), families known to have specific detrital roles in accelerating nutrient-recycling [62] and consuming dead organisms in both adult and larval stages, respectively. Our data show that mixed-grass–forb prairies hosted a greater biomass of detritivores than corn or switchgrass (Table 1) but that landscape context and patch size influenced responses. Specifically, detritivore biomass declined with patch size and increased with land cover diversity.

An important caveat to our study is the use of a single method (sweep netting) to sample arthropod groups with diverse behaviors, movement patterns, and microhabitats. Bee bowls, for example, are a preferred method for obtaining less-biased sampling of pollinator communities, and pit traps would have provided more information about terrestrial and soil-dwelling taxa. In addition, because we sampled the arthropod community during early- to mid-summer, the scope of inference of our study is limited to a relatively narrow time-period (but see [20]).

These results, collected over a large region, corroborate a considerable body of plot-scale work on the benefits of polycultures and habitat diversity on arthropod populations [63]. Specifically, we found that arthropod diversity and biomass was influenced by within-field plant diversity, patch size, and landscape-scale habitat structure and composition. In their examination of how arthropod predators and herbivores respond to alternative agroenergy plantings, Werling et al. [21] treated perennially based plantings as a single category varying in floristic diversity. They found moderate levels of plant diversity provided substantial benefits to predator and herbivore diversity in this study region. Collectively, selection of perennial feedstocks with moderate levels plant diversity and a substantial forb component will be likely to enhance the diversity and biomass of arthropods. Because arthropod richness is generally linked to habitat stability (annual vs. perennial) and floristic diversity [8], these within-field patterns have been anticipated and previously observed in small subsets of the arthropod community [23].

The landscape effects we documented suggest that expansion of biofuel production could affect biodiversity by driving changes in the area of perennial habitats.

Conversion of forest or other perennial habitats to intensively managed row crops is likely to reduce arthropod biodiversity in agricultural landscapes while the planting of next-generation perennial-based crops could enhance it. Economically important ecosystem services like pollination and pest control should be similarly affected [14, 21, 23]. Perennial habitats likely provide limiting resources that are unavailable in annual crops [7] such that crop selection that increases the extent of these habitats is more important in shaping biodiversity responses than crop placement that shapes the extent or configuration of more resource-poor annual crops. Importantly, the majority of fields we sampled were not under management for biomass production. Because crop management, including biomass removal, harvest, and the application of chemicals, will affect vegetation structure in fields and likely shape the availability of resources (e.g., detritus availability), our data likely overestimate the benefits of perennial biomass crops for arthropod diversity and biomass. Neither did our broad sampling methods target focal groups (e.g., bees) and all important spatial niches (e.g., ground), which may leave some functionally important taxa (e.g., carabids) poorly sampled. Finally, we did not sample belowground arthropod communities, which are likely to have more influential roles than aboveground arthropods in processes such as decomposition [49] and herbivory [64] that may have a greater impact on plant populations [56, 64].

Intensification of bioenergy production on agricultural land in North America over the last decade [65] has contributed to the increasing homogenization of agricultural landscapes [8] which is considered an important mechanism underlying the loss of biodiversity and ecosystem services in agrarian regions [5, 14]. Maximizing arthropod biodiversity and arthropod-mediated ecosystem services in future agricultural landscapes will require an understanding of the role of crop placement and landscape context [14, 17]. With economic incentives for corn ethanol production in the USA driving the rapid expansion of corn production [11], coinciding reductions in land cover diversity and biocontrol services in nearby agricultural fields have been documented [8, 23]. Importantly, these changes are predicted to increase pesticide requirements, further eroding the suitability of agricultural landscapes for beneficial arthropods [14, 66]. Perennial-based crops are projected to have reduced pesticide and fertilizer demands, longer rotation periods that reduce disturbance, and greater structural heterogeneity that more closely resembles native ecosystems [22, 26]. Biocontrol services associated with arthropod predators [8, 21] may further minimize the need for pesticides provided that conducive management practices such as asynchronous harvest of neighboring fields or increased periods between harvests are implemented to allow recolonization by beneficial arthropods after harvests [22, 67]. Because fields that are 60–100% grass are equally digestible by refineries

[68], integration of a forb component into production systems may become economically feasible as a means of enhancing natural biocontrol. The economic viability of diverse perennial monocultures will ultimately need to be assessed through an accounting of the trade-offs among the value of services like biocontrol and pollination, biomass production, and the cost and environmental consequences of herbicides. Yet, second-generation biofuel crops stand to make significant contributions to the conservation of biodiversity and the ecologically and economically important services they provide.

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