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Perennial biomass feedstocks enhance avian diversity

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Abstract

Federal mandates to increase biofuel production in North America will require large new tracts of land with potential to negatively impact biodiversity, yet empirical information to guide implementation is limited. Because the temperate grassland biome will be a production hotspot for many candidate feedstocks, production is likely to impact grassland birds, a group of major conservation concern. We employed a multiscaled approach to investigate the relative importance of arthropod food availability, microhabitat structure, patch size and landscape-scale habitat structure and composition as factors shaping avian richness and abundance in fields of one contemporary (corn) and two candidate cellulosic biomass feedstocks (switchgrass and mixed-grass prairie) not currently managed as crops. Bird species richness and species density increased with patch size in prairie and switchgrass, but not in corn, and was lower in landscapes with higher forest cover. Perennial plantings supported greater diversity and biomass of arthropods, an important food for land birds, but neither metric was important in explaining variation in the avian community. Avian richness was higher in perennial plantings with greater forb content and a more diverse vegetation structure. Maximum bird species richness was commonly found in fields of intermediate vegetation density and grassland specialists were more likely to occur in prairies. Our results suggest that, in contrast to corn, perennial biomass feedstocks have potential to provide benefits to grassland bird populations if they are cultivated in large patches within relatively unforested landscapes. Ultimately, genetic improvement of feedstock genets and crop management techniques that attempt to maximize biomass production and simplify crop vegetation structure will be likely to reduce the value of perennial biomass plantings to grassland bird populations.

Keywords: agroenergy, biodiversity, Biofuels, cellulosic bioenergy, grassland birds, switchgrass

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Dedicated bioenergy crops have emerged as an essential component of North American and European sustainable energy policies because they offer the potential to provide a renewable source of energy and petroleum-based commodities (e.g. plastics) while economically stimulating the agricultural sector. Federal mandates for corn ethanol and cellulosic biofuel production in the United States (Energy Independence and Security Act – US Congress 2007) are projected to greatly expand the acreage of land under cultivation as well as intensify the management of current agricultural lands (West *et al.*, 2009). The expansion and intensification of agricultural systems is widely recognized as a major driver of global biodiversity loss (Hails, 2002; Green *et al.*, 2005). As such, serious concerns have been raised about the consequences of increasingly biofuel-dominated landscapes to animal populations (Robertson *et al.*, 2008; Fargione *et al.*, 2009; Fletcher *et al.*, 2010), especially where biomass production could impact sensitive and less-developed areas and displace native habitats (Groom *et al.*, 2008). In North America, bioenergy crops are predicted to disproportionately impact the grassland biome (McDonald *et al.*, 2009) where agriculture has almost entirely replaced once-dominant temperate grassland ecosystems and dramatically reduced and

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endangered animal populations. Consequently, assessing the projected biodiversity impacts of new bioenergy crops will be critical to reconciling the demands of biodiversity conservation and agricultural production (Butler *et al.*, 2007). Whether the emerging biofuel economy will further compromise biodiversity or provide opportunities for biodiversity conservation remains unclear, in large part due to the paucity of empirical studies directly comparing the ability of alternative biomass crops to support native animal species (Fargione *et al.*, 2009).

To date, over 30 plant species have been proposed as biofuel feedstocks or are currently grown for biofuels in North America. Corn ethanol is presently the most important biofuel crop in North America and federal import tariffs and production subsidies continue to encourage its expansion to meet production mandates (US Congress, 2007). Because animal biodiversity in corn fields is generally low, expansion of corn at the expense of other crops or seminatural habitats is predicted to lead to biodiversity losses (Murray *et al.*, 2003; Fletcher *et al.*, 2010; Gardiner *et al.*, 2010).

Proposed second-generation (cellulosic) bioenergy crops include various grass and forbs species that produce high annual yields of biomass (Perlack *et al.*, 2005) and that may be directly burned to generate electricity or processed to produce a variety of liquid fuels and other products (Ragauskas *et al.*, 2006). Switchgrass (*Panicum virgatum*), a perennial warm-season grass native to the North American Tallgrass Prairie, has been selected as a model energy crop by the US Department of Energy (McLaughlin & Walsh, 1998). Compared with row crops, switchgrass monoculture appears to support a relatively high diversity of beneficial arthropods (Gardiner *et al.*, 2010) and can provide habitat for some grassland specialist bird species (Murray & Best, 2003; Roth *et al.*, 2005; Bakker & Higgins, 2009). Recent research has demonstrated that so-called 'low-input, high-diversity' crops such as mixed-grass prairie reconstructions may also act as a sustainable source of biomass (Tilman *et al.*, 2006). Research across many areas has demonstrated that plant species diversity is linked to greater animal biodiversity (Haddad *et al.*, 2001; Sullivan & Sullivan, 2006; Gardiner *et al.*, 2010), suggesting that mixed-species production systems should support the most diverse animal assemblages of all candidate biomass crops. If widely adopted, perennial biomass crops could, then, fundamentally change the structure and composition of agricultural landscapes with the potential to enhance the conservation of grassland biodiversity.

Here, we report on a field study designed to fill this knowledge gap. We ask if alternative bioenergy feedstocks differ in their ability to support diverse and abundant populations of grassland birds which have experienced more dramatic and rapid population declines than any other group of North American birds (Sauer *et al.*, 2008). We compare the species richness, species density, and abundance of grassland birds in corn and two candidate cellulosic feedstocks crops: switchgrass and mixed prairie. Specifically, we ask if these alternatives can be ranked in terms of their value to bird communities and, if so, how arthropod food availability and components of habitat structure and composition at multiple spatial scales (microhabitat, patch and landscape) relate to avian diversity and abundance. The generally positive relationship between plant diversity and biodiversity suggests that mixed-grass prairie should host the most diverse avifauna. Because grassland bird species are adapted to particular ranges of microhabitat habitat conditions (Wiens 1969; Renken & Dinsmore, 1987; Herkert, 1994), we expect that bird diversity in structurally more complex switchgrass monocultures should exceed that of corn. Other factors that may play important roles in shaping grassland bird distributions include the availability of food (Zanette *et al.*, 2000), patch size (Herkert, 1994; Vickery *et al.*, 1994; Winter & Faaborg 1999) and the structure and composition of the surrounding landscape (Bakker *et al.*, 2002; Cunningham & Johnson, 2006; Renfrew & Ribic, 2008).

Methods

Study design and site selection

Twenty sites of each of three treatments (corn, switchgrass, and mixed-grass prairie) were selected from preexisting fields throughout southern Michigan over the 2-year course of this study (Fig. 1). We visited 39 sites in 2008 (corn = 8, prairie = 16, switch = 15), 39 sites in 2009 (corn = 12, prairie = 13, switch = 14), and surveyed a subset of sites in both years (corn = 0, prairie = 9, switchgrass = 9) to examine interannual variation in the avian community. Markets for cellulosic biomass have not yet been established and research to improve crop genets (e.g. maximizing biomass) and determine optimal species combinations for the production of polycultures is ongoing. Because perennial biomass crops are not yet managed for production, research investigating actual cropping systems is not yet possible. Instead, we chose to investigate within-field vegetation characteristics we felt were most likely to be affected by feedstock selection and crop management while also relevant to bird community composition: (1) vegetation height and density, (2) grass and forb composition, and (3) within-field variation in vegetation structure. Two switchgrass fields in this study were

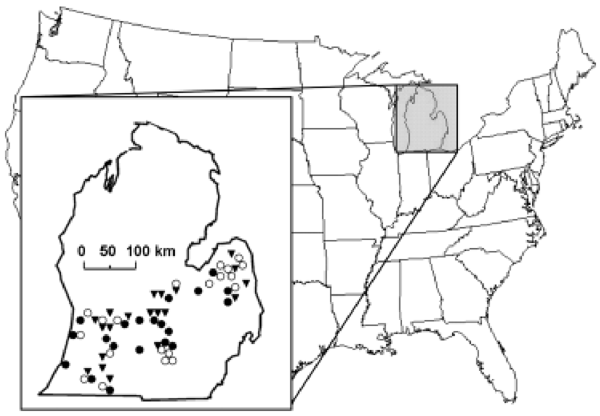

Fig. 1 Map of the study region in the southern peninsula of Michigan. Locations of mixed-grass prairie (filled circles), switchgrass (open circles) and corn (triangles) fields (n = 20 each) where the bird community was sampled are indicated.

actively managed for biomass production. The remaining prairie and switchgrass sites were managed for wildlife habitat or as native community reconstructions. As such, switchgrass fields were rarely strict monocultures. For each feedstock we selected sites representing a range of vegetation density and stand structural heterogeneity from within landscapes varying as much as possible in the amount of non-crop habitat they contained. Because we wished to examine the importance of patch size in shaping avian communities, we also selected patches to vary as widely as possible in size (corn: 5–73 ha; prairie: 2–101 ha; switchgrass: 2–37 ha). Study fields were located a minimum distance of 5 km from other sites.

Bird Surveys

We surveyed the bird community associated with fields, making two visits to each patch: (1) 22 May–20 June and (2) 16 June–4 July. Species richness and abundance were estimated based on two survey techniques: fixed-width transects and area searches. Fixed-width transects (Emlen, 1977) were 50 m long by 50 m wide. Two observers conducted bird surveys during the first 4 h after sunrise, slowly walking a line bisecting transects and visually or aurally identifying all individuals foraging, perching or vocalizing within transects, excluding flyovers. To obtain representative samples of fields differing in area while avoiding pseudo-replication (reviewed in Ribic *et al*., 2009), 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 before 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. Grassland bird communities exhibit 'area-sensitivity', or higher species richness per unit area in larger habitat patches in mixed-grass prairies in this region (Herkert, 1994). We calculated median values of transect-scale species richness (species richness per unit area; hereafter species density) and abundance at the patch scale, combining information from all site visits. We used species density as a metric to test the hypothesis that avian communities are also area-sensitive in corn and switchgrass cover types.

To estimate patch-scale species richness, we area searched portions of each field not covered by transects. We maintained observer effort proportional to patch size by having two observers walk at a regular pace though each field in a systematic pattern such that two observers simultaneously passed within 50 m of every point in a field. We pooled species detected during strip-transect surveys (including those detected at distances > 50 m) with area search detections.

Within-patch vegetation structure and composition

During the first site visit, within-field vegetation structure was characterized within each 50 m-long transect to determine how microhabitat gradients may affect spatial distributions of birds. Within each transect, we randomly selected five nonoverlapping sampling points at which we recorded vertical density of vegetation, litter depth, and canopy coverage. Vertical density (an index of biomass, Harmoney *et al*., 1997) was quantified as the minimum height of visual obstruction by vegetation from 4 m in each cardinal direction on a Robel pole at a height of 1 m (Robel *et al*., 1970). Canopy coverage was assessed on the basis of non-overlapping percentages of forbs, grass and standing dead vegetation visible from directly above within a Daubenmire quadrat (Daubenmire, 1959). Ground cover within a quadrat was quantified as the non-overlapping percentages of bare ground and litter. Cover estimates were assigned a numerical index associated with coverage ranges (1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, 6 = 95–100%). We computed mean values at the patch scale and calculated a patch-scale index of microhabitat heterogeneity designed to represent habitat features a ground-dwelling bird might use in assessing patchiness (Wiens, 1974).

Patch and landscape variables

Settlement behavior in grassland birds is frequently linked to landscape composition at 1500 m-radius and smaller scales (e.g. Ribic & Sample, 2001; Bakker *et al*., 2002; Renfrew & Ribic, 2008). We derived landscape characteristics within a 0.5 and 1.5 km radius of each study site using the 2009 Cropland Data Layer (56 m resolution) (USDA, 2010). Patches were categorized as containing cropland (e.g. corn, soybeans), herbaceous perennial habitats (including grasslands), forest, urban land (>60% impervious surface). All other land cover classes were pooled into a fifth category (<1% of total area) not used in analyses. Observers directly verified the accuracy of land-use categories during site visits. We calculated the proportion of the landscape within 0.5 and 1.5 km of each site in these cover types using ARCGIS 9.3 (ESRI, 2008) and used the PATCH ANALYST 4.0 extension to ARCGIS to calculate a modified Simpson's Diversity Index (Rempel, 2010).

We used principal components analysis with orthogonal rotation to reduce the number of vegetation structural and landscape-scale variables into component variables. The first microhabitat component (MPC1) accounted for 86% of the total variation (eigenvalue 3.464) and described a gradient of increasing vegetation density, percentage of standing dead vegetation and ground coverage of litter (Appendix S1). Mean forb cover (FORB) was uncorrelated with other microhabitat variables and so was retained as a separate independent variable. The first landscape principal component (LPC1) accounted for 47% of the total variation (eigenvalue 1.89) and described a gradient of increasing forest cover and reduced crop cover. The second landscape component (LPC2) accounted for 29% of the total variation (eigenvalue 1.1) and described a gradient of increasing urbanization and reduced open and semi-natural habitats including perennial grasslands, pastures and oldfields. Because we found a strong correlation in the principal components LPC1, LPC2, and MHET between spatial scales ($r^2 = 86\%$, 89%, and 77%, respectively) we analyzed data using variables assessed only at the 1500 m-radius, a scale at which grassland birds commonly respond to landscape structure (Bakker *et al.*, 2002; Renfrew & Ribic, 2008).

Arthropod diversity and abundance

Terrestrial arthropods represent an important food source for breeding birds that can affect habitat selection (Martin, 1987). During the first site visit we sampled terrestrial arthropods via sweep net samples of aboveground vegetation at the geographic center of each field. Each of two within-patch sweep samples began at a distance of 50 m in opposite directions from the field center, moving toward the center point. Fifty sweeps per sample allowed two spatially separated sweep sampling lines to be placed within each field. Arthropods were placed in sealed plastic bags and transferred to 90% ethanol solution for storage. We identified individuals to the family level, measured body length, estimated individual mass using published length-regression estimates (Hódar, 1996) and then computed total arthropod biomass at the patch-level. Patch-scale estimates of arthropod family richness were obtained using the Chao 2 asymptotic richness estimators in EstimateS (Colwell, 1997).

Statistical analysis

We generated a detection probability for each bird species recorded ≥ 10 times within each feedstock and we combined count data over both years to increase sample size and because detection probabilities (were similar between years ($P > 0.05$). We then tested for potential differences in detection probability between feedstocks using ANOVA.

We used an information-theoretic model selection approach to determine the relative importance of nine environmental variables in explaining the following attributes: (1) richness, species density and abundance of species known to breed in a particular habitat type and (2) abundance and occurrence of grassland obligate species. Species were considered grassland obligates based on published research demonstrating that their breeding habitat is entirely or largely restricted to natural or seminatural grassland habitat (sensu Vickery *et al.*, 1999, see Table 1), and breeders if we found published evidence of breeding in a given feedstock type (FEED) or if we incidentally located a nest during the course of our surveys. The nine explanatory variables included (1) microhabitat principal component 1 (MPC1), (2) a quadratic function of MPC1 ($MPC1^2$), (3) microhabitat structural heterogeneity (MHET), (4) landscape principal component 1 (LPC1), (5) landscape principal component 2 (LPC2), (6) patch size (PSIZ), (7) Simpson's index of land cover diversity (LDIV), (8) terrestrial arthropod biomass (AMAS), and (9) terrestrial arthropod family richness (ARIC). Because species richness generally increases with patch size in an asymptotic and nonlinear fashion (Rosenzweig, 1995), we log transformed the patch size before analysis. To test for differences among years in community richness or abundance that could bias model selection, we conducted paired *t*-tests on community richness and abundance at sites visited in both years of the study.

Because count data typically follow a non-normal distribution, we modeled avian community metrics using generalized linear models with a Poisson distribution and log-link function using SPSS version 15 (SPSS, 2006). For sites that were resurveyed in the second year, we took the mean value of all explanatory variables and median values of avian count metrics, giving observations twice the weight in analyses. Because cornfields exhibit significant vegetation structural differences

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Table 1 List of species detected in corn, switchgrass and prairies ($n = 20$ each) in southern Michigan

Species	Corn	Switch	Prairie
American Crow (*Corvus brachyrhynchos*)	X		
American Goldfinch (*Spinus tristis*)	X	**X**	**X**
American Robin (*Turdus migratorius*)	X	X	X
Baltimore Oriole (*Icterus galbula*)			X
Barn Swallow (*Hirundo rustica*)	X	X	X
Brown-headed Cowbird (*Molothrus ater*)	**X**	**X**	**X**
Blue Jay (*Cyanocitta cristata*)	X		X
Bobolink (*Dolichonyx oryzivorus*)*		**X**	**X**
Brown Thrasher (*Toxostoma rufum*)	X		X
Clay-colored Sparrow (*Spizella pallida*)		**X**	
Chipping Sparrow (*Spizella passerina*)	X	X	X
Chimney Swift (*Chaetura pelagica*)	X	X	X
Common Grackle (*Quiscalus quiscula*)	X	X	X
Cooper's Hawk (*Accipiter cooperii*)			X
Common Yellowthroat (*Geothlypis trichas*)		**X**	**X**
Dickcissel (*Spiza americana*)*			**X**
Eastern Bluebird (*Sialia sialis*)	X	**X**	**X**
Eastern Kingbird (*Tyrannus tyrannus*)	X	**X**	**X**
Eastern Meadowlark (*Sturnell magna*)*		**X**	**X**
European Starling (*Sturnus vulgarus*)	X	X	X
Field Sparrow (*Spizella pusilla*)	X	**X**	**X**
Great Blue Heron (*Ardea herodias*)		X	X
Grey Catbird (*Dumetella carolinensis*)	X		
Grasshopper Sparrow (*Ammodramus savannarum*)[1]*	**X**	**X**	**X**
Henslow's Sparrow (*Ammodramus henslowii*)[1,2]*		**X**	**X**
House Finch (*Carpodacus mexicanus*)		X	
Horned Lark (*Eremophila alpestris*)	**X**		**X**
House Sparrow (*Passer domesticus*)		X	X
Indigo Bunting (*Passerina cyanea*)		X	X
Killdeer (*Charadrius vociferus*)	**X**	**X**	**X**
Mallard (*Anas platyrhynchos*)		**X**	**X**
Mourning Dove (*Zenaida macroura*)	X	**X**	**X**
Northern Bobwhite (*Colinus virginianus*)			**X**
Northern Cardinal (*Cardinalis cardinalis*)			X
Northern Flicker (*Colaptes auratus*)	X		X
Northern Harrier (*Circus cyaneus*)[1]*			**X**
Ring-necked Pheasant (*Phasianus colchicus*)		**X**	**X**
Red-tailed Hawk (*Buteo jamaicensis*)	X	X	
Ruby-throated Hummingbird (*Archilochus colubris*)			X
Red-winged Blackbird (*Agelaius phoeniceus*)	X	**X**	**X**
Sandhill Crane (*Grus canadensis*)	X		X
Savannah Sparrow (*Passerculus sandwichensis*)*	**X**	**X**	**X**
Sedge Wren (*Cistothorus platensis*)*		**X**	**X**
Song Sparrow (*Melospiza melodia*)	X	**X**	**X**
Swamp Sparrow (*Melospiza georgiana*)		**X**	
Tree Swallow (*Tachycineta bicolor*)	X	X	X
Turkey Vulture (*Cathartes aura*)	X	X	X
Upland Sandpiper (*Bartramia longicauda*)*		**X**	
Vesper Sparrow (*Pooecetes gramineus*)*	**X**	**X**	
Willow Flycatcher (*Empidonax traillii*)			X
Wild Turkey (*Meleagris gallopavo*)	X		**X**
Yellow Warbler (*Dendroica petechia*)			X
Totals	29 (6)	35 (22)	45 (23)

Species names in bold and species totals in parentheses represent those for which published research or field observations indicated evidence of breeding in a respective crop. Obligate grassland species*, species with conservation status in the state of Michigan[1] and species appearing on the Audubon Watchlist[2] (Audubon 2007) are indicated.

from switchgrass and prairie, we first conducted analyses involving all three habitat types, then followed with a second set of analyses excluding bird observations in cornfields and including FORB as an explanatory variable. For prediction of obligate species abundance based on median values we used zero-inflated models (Lambert, 1992) because count data frequently contained zeros. The likelihood of detecting obligate species was modeled using binary logistic regression (Hosmer & Lemeshow, 1989).

We developed a set of *a priori* candidate models that reflected our assessment of likely causes of variation in community metrics, including models of each explanatory variable alone, and two- three- and four-variable variable models that we determined to be ecologically relevant. Because species–area relationships may differ by feedstock, we also included models with interactions between patch size and feedstock type. We evaluated the degree of support for logistic and zero-inflated models using Akaike's second-order information criterion (AIC_c; Akaike, 1973), which includes a small-sample bias adjustment, and used $QAIC_c$ (quasi-AIC_c) which accounts for potential overdispersion in count data (Burnham & Anderson, 2002). We selected the best model(s) by judging the degree of support as indicated by ΔAIC_c or $\Delta QAIC_c$ and normalized Akaike weights. We considered models with ΔAIC_c or $QAIC_c \leq 2$ to have substantial support and models with ΔAIC_c or $QAIC_c > 2$ and ≤ 4 to have little to no empirical support (Burnham & Anderson, 1998). Fit of global generalized linear models (models including all factors) was estimated as (deviance/df), which is close to 1 if the Poisson distribution is a good fit. Model fit of the global logistic regressions were assessed with a goodness of fit test (Hosmer & Lemeshow, 1989). We used Pearson's correlations to identify the direction of each metric's relationships with predictor variables and plotted the relationship between dependent and independent variables using model-averaged parameter estimates (Burnham & Anderson, 2002).

Results

Bird community composition

In total, we detected 52 species of birds, with the greatest total and breeding species richness in prairie (total = 45; breeding = 23), followed by switchgrass (total = 35; breeding = 22), and cornfields (total = 29; breeding = 6, Table 1). Because no species were detected ≥ 10 times in all three feedstocks, comparisons of detection probability among habitats were all between prairie and switchgrass. Detection probability varied across species, but the estimated proportion of birds detected with 50 m was close to 100% (range = 0.91–1.00), and didn't differ between feedstocks for any species (all $P > 0.17$). Several species of high state and national conservation status (e.g. Henslow's Sparrow, Grasshopper Sparrow and Northern Harrier, Table 1) were found in both switchgrass and prairie plots. We found territorial Savannah and Grasshopper Sparrows in a single cornfield that had been planted with a fall cover crop of squash. No detectable, consistent year-to-year difference in breeding species richness ($t = 0.44$, df = 17, $P = 0.66$) or abundance ($t = 0.27$, df = 17, $P = 0.27$) were evident across study plots.

Arthropod diversity and abundance

We captured 21 596 individual arthropods. Mean arthropod biomass and richness were highest in prairie followed by switchgrass and corn (Table 2).

Vegetation structure and composition

Microhabitat principal component 1 was highest in switchgrass patches, indicating a marginally higher density of vegetation, but the heterogeneity of stand structure in switchgrass patches was generally comparable to that of prairie (Table 2). Forb cover in switchgrass plots was intermediate to other crops, indicating switchgrass fields had been invaded to varying degrees. The range of values for landscape-scale habitat variables were generally comparable across crop types (Table 2).

Avian community: all crops

Global models provided a good fit to the data (Appendix S2). Considering all feedstocks, top models of breeding species richness and species density were influenced by feedstock type (FEED) and patch size (PSIZ, Table 3). Species richness and species density exhibited a positive relationship with patch size in switchgrass and prairie, but not in corn (Figs. 2A and B). A quadratic effect of microhabitat principal component 1 ($MPC1^2$), reflecting increasing density and height of vegetation) was negatively related to breeding species richness (Fig. 3), indicating maximum overall richness at intermediate values of MPC1. One model of breeding species density indicated a positive relationship with MPC1.

The most important variables predicting abundance were feedstock type, LPC1, and $MPC1^2$ (Table 3). A single model stood out (ΔAIC_c or $\Delta QAIC_c < 2$), for both abundance metrics. The best model of breeding bird abundance predicted higher numbers in prairie and switchgrass than in corn (prairie/switch: 3.9 indivi-

Table 2 Summary descriptions of explanatory variables from prairie, switchgrass and corn ($n = 20$ each) fields in southern Michigan sampled in 2008 and 2009

Variable		Corn	Switchgrass	Prairie	$F_{2,57}$	*P*
Within-patch						
MHET	Microhabitat heterogeneity index (0–2)	1.2 (1.2)	0.7 (0.3)	0.8 (0.4)	2.56	0.09
MPC1	Microhabitat principal component 1	−0.2 (0.2)^a	0.8 (0.6)^b	0.4 (0.4)^c	127.90	< 0.001
AMAS	Arthropod biomass (g/sample)	0.03 (0.04)^a	0.2 (0.1)^b	0.57 (0.35)^c	34.54	< 0.001
ARIC	Arthropod richness (# families/sample)	20.5 (14.3)^a	59.3 (24.0)^b	77.2 (22.2)^c	39.48	< 0.001
FORB	Mean % forbs (1–6)	1.2 (0.4)	1.3 (0.7)	1.7 (0.5)	1.83	0.17
Patch- and landscape-scale						
PSIZ	Patch size (ha)	18.5 (15.7)	6.5 (5.7)	18.6 (22.9)	2.64	0.08
LPC1	Landscape principal component 1	−0.0.2 (1.0)	0.03 (0.9)	0.2 (1.1)	0.57	0.57
LPC2	Landscape principal component 2	0.1 (1.3)	0.0 (1.0)	−0.1 (0.6)	0.26	0.77
LDIV	Landscape diversity (0–1)	0.6 (0.1)	0.7 (0.1)	0.6 (0.1)	2.22	0.12

Means are given with standard deviations in parentheses. Critical and significance values of ANOVAs comparing mean values among habitats are given. Letters indicate significant differences ($P < 0.05$) among habitat-based means based on Tukeys LSD test. Microhabitat heterogeneity describes within-field variation in the vertical density of vegetation. Landscape diversity represents Simpson's index of habitat diversity (1500 m radius) surrounding a focal patch.

Table 3 Models of avian species richness, species density, abundance, and occurrence associated with surveys at corn, switchgrass and prairie (n = 20 each) fields in southern Michigan

Community metric	Model	K*	ΔAIC_c or $\Delta QAICc$	w_i†
Breeding species richness	FEED × PSIZ	4	0.00	0.21
	FEED × PSIZ–MPC1^2	5	0.52	0.16
	FEED + PSIZ	3	0.99	0.13
Breeding species density	FEED × PSIZ	4	0.00	0.16
	FEED + PSIZ	3	0.56	0.12
	FEED + PSIZ + MPC1	4	0.61	0.12
Breeding species abundance	FEED−LPC1	3	0.00	0.48
Obligate species abundance	−MPC1^2	2	0.00	0.86
Obligate species occurrence	FEED + LPC1−MPC1^2	4	0.00	0.36
	PSIZ−MPC1^2 + MHET	4	1.10	0.21

*Number of parameters in a model.

†Model Akaike weight.

The table lists competing models ($\Delta QAIC_c$ or $\Delta AIC_c < 2.00$) for (1) breeding bird species and (2) obligate grassland birds. Response variables are summarized in methods and Table 2. Models with interaction terms are denoted with a multiplication symbol (×) but intercept terms are not listed.

duals/transect; corn: 0.9 individuals/transect), and abundance was negatively linked to LPC1. MPC1^2 was the most important variable explaining obligate species abundance, indicating maximum abundance at intermediate levels of microhabitat density. Obligate occurrence was also linked negatively to MPC1^2 and LPC1, positively to microhabitat heterogeneity (MHET) and patch size, and to feedstock (2.01 times more likely to occur in prairie/switchgrass than in corn).

Avian community: prairie and switchgrass

Global models without data from corn fields also fit the data set well (Appendix S2). Patch size continued to be positively related to breeding species richness and species density in switchgrass and prairie, and feedstock (FEED) was also important in competing models of breeding species density (Table 4). One model indicated higher breeding species density in prairie (2.4 species/transect) than in switchgrass (1.6 species/transect), while a second contained an interaction between PSIZ and FEED indicating that species accumulate with patch size more slowly in switchgrass (slope = 0.48 species/log hectare) than in prairie (slope = 0.91 species/log hectare). One model each positively linked microhabitat heterogeneity and LPC2 to breeding species richness, and one linked forb cover positively with species density.

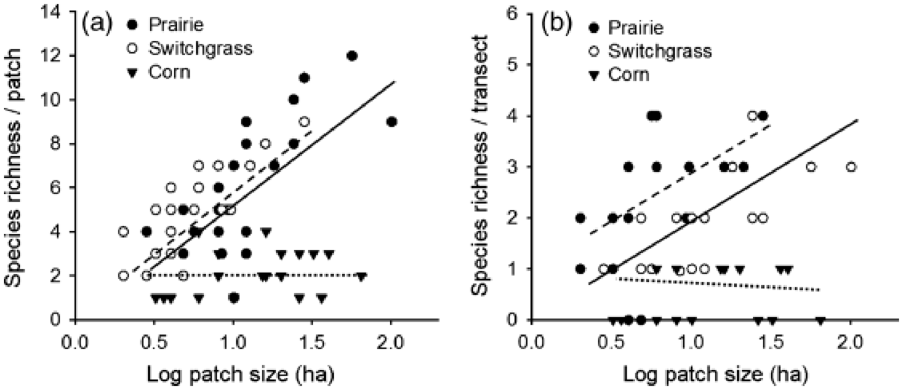

Fig. 2 Partial regressions of (log) patch size of biofuel crop fields vs. bird species richness (a), and species density (b). Parameter estimates are based on model-averaged values. The slope of the regressions explaining richness in prairie (filled circles, solid lines) and switchgrass (open circles, dashed lines) are not significantly different (both $P > 0.36$), but are greater than corn (triangles, dotted lines).

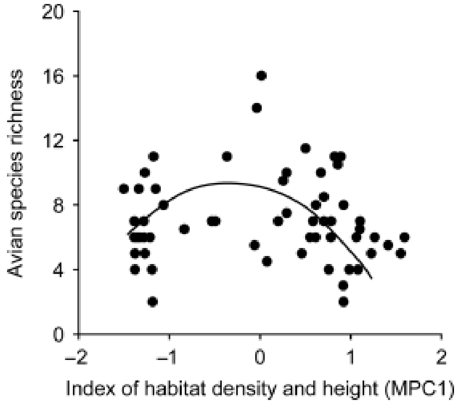

Fig. 3 The quadratic relationship between habitat structure and breeding bird species richness in 60 patches of 3 feedstock plantings in southern Michigan. Increasing values of microhabitat principal component one (MPC1) indicate patches with increasing density and height of vegetation, standing dead vegetation and increasing litter depth.

Competing models indicated that breeding species abundance was a negative function of increasing landscape forest cover (LPC1), and a positive function of increasing urbanization (LPC2) and forb cover. One model with high weight ($w_i = 0.99$) explained obligate species abundance as a negative function of LPC1 and MPC1^2, indicating maximum abundance at intermediate levels of vegetation density located in unforested landscapes. Competing models indicated the likelihood of obligate species occurring was greater in larger patches of prairie (1.7 times more likely) in less forested landscapes. In an ancillary set of analyses, results of model selection based on mean values of community metrics and analyzed with general linear models were qualitatively similar, and top models for community metrics in both (all crop and no corn) analyses emphasized the same important explanatory variables.

Discussion

This is the first empirical study to directly compare avian diversity responses to a suite of alternative biomass feedstocks, and the first study of grassland bird communities to simultaneously assess the importance of microhabitat, patch and landscape-scale variables among different habitat types. Various authors have examined how focal species respond to patch size and habitat features at different spatial scales and have found that only some species appear to respond positively to habitat area, while others are more restricted by habitat structure or the composition of the surrounding landscape (Herkert, 1994; Bakker *et al.*, 2002; Davis 2004; Cunningham & Johnson, 2006; Renfrew & Ribic, 2008). We focused our efforts on conservation-relevant subsets of the avian community to best understand how feedstock selection and the structure and composition of habitat elements that can be affected by biomass crop management and placement may more broadly affect grassland bird populations in agricultural landscapes. We found that perennial plantings supported more diverse and abundant avian communities and that vegetation structure and composition at several spatial scales were important factors shaping the responses of grassland birds to different plantings.

Species richness and area sensitivity

The most common breeding species in corn fields were Killdeers and Horned Larks, while prairie and switchgrass plantings shared a similar and larger pool of species (Table 1). Grassland species of conservation concern (e.g. Henslow's Sparrow) primarily occurred in switchgrass and prairie fields. Some competing models indicated greater breeding species density in prairie than switchgrass and obligate grassland birds were

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Table 4 Models of avian species richness, species density, abundance, and occurrence associated with surveys at mixed-grass prairie and switchgrass sites ($n = 20$ each) in southern Michigan

Community metric	Model	K*	ΔAIC_c or $\Delta QAICc$	w_i†
Breeding species richness	PSIZ	2	0.00	0.23
	PSIZ−MHET	3	1.07	0.14
	PSIZ + LPC2	3	1.07	0.14
Breeding species density	FORB	2	0.00	0.10
	FEED × PSIZ	4	0.30	0.09
	FEED + PSIZ	3	0.45	0.08
Breeding species abundance	FORB−LPC1 + LPC2	4	0.00	0.19
	−LPC1 + LPC2	3	1.24	0.10
	FORB−LPC1	3	1.50	0.09
Obligate species abundance	−MPC1^{2}−LPC1	3	0.00	0.99
Obligate species occurrence	PSIZ−LPC1	3	0.00	0.35
	FEED + PSIZ	3	0.19	0.32

*Number of parameters.

†Model Akaike weight.

Following Table 3, the table lists competing models ($\Delta QAIC_c$ or $\Delta AIC_c < 2.00$) for (1) breeding bird species and (2) obligate grassland birds. Response variables are described in the methods and Table 2. Models with interaction terms are denoted with a multiplication symbol (×) but intercept terms are not listed.

more likely to occur in mixed-grass plantings (Table 4), but richness and abundance were generally similar in prairie and switchgrass fields.

Area sensitivity, in which the pattern of a species' occurrence and/or density increases with patch area (Robbins *et al*., 1989), is a characteristic of many grassland birds that can lead to increased species richness and density at the community level (Herkert, 1994). We found an increase in both species richness (Fig. 2a) and species density (Fig. 2b) in prairie and switchgrass, but not in corn fields. Obligate grassland birds were most likely to be found in larger patches of perennial feedstocks. These patterns suggest perennial large perennial biomass plantings could accrue some biodiversity benefits unrealized in corn. Collectively, these results suggest that by contributing a unique avifuanal component, perennial biomass feedstocks such as switchgrass and mixed prairie have potential to increase beta-diversity in agricultural landscapes when chosen in favor of corn.

Landscape composition and structure

Grassland birds commonly respond to habitat features outside of their focal habitat patch (Ribic *et al*., 2009). Woody vegetation (e.g. crop borders, forest) in the surrounding landscape have been associated with a lower density of grassland birds in a focal patch (Coppedge *et al*., 2001; Ribic & Sample, 2001; Bakker *et al*., 2002; Cunningham & Johnson, 2006; Winter *et al*., 2006; Renfrew & Ribic, 2008). Avoidance behavior appears to be strongly related to landscape forest composition at larger spatial scales (1000–1500 m radius) whereas the configuration of land cover types appears less important (Ribic & Sample, 2001; Bakker *et al*., 2002; Renfrew & Ribic, 2008). In this study, competing models of abundance and occurrence frequently indicated a negative relationship with the area of forested land cover (1500 m radius scale) surrounding all planting types. While the mechanism(s) driving the avoidance of forest may differ among taxa, the pattern itself dictates that production of switchgrass and mixed prairie for biomass aimed at increasing avian biodiversity should target largely unforested regions. Production of dedicated bioenergy crops will likely be concentrated in the immediate vicinity of power stations or cellulosic ethanol refineries to minimize transportation costs. Economic concerns may, then, favor the spatial concentration of perennial biomass crops into local agricultural landscapes that are highly attractive to breeding and obligate grassland birds because of their high proportion of grassland and low proportion of forest cover, thus creating an opportunity for biodiversity goals.

Some grassland birds inhabit small patches as long as they are embedded within landscapes with a high percentage of grassland cover (Bakker *et al*., 2002). In this study, landscape-scale variables were a largely associated with models of abundance in perennial habitats. Higher breeding species diversity and abundance in perennial plantings was positively linked with landscape principal component 2, indicating more urbanized land cover and reduced cover of open habitats including oldfields, grasslands and pastures. Resolving this result with previous research is difficult. While the percentage of open habitats in our study landscapes exhibited significant variation (mean = 6.98%, range 0–49%), most variation was associated with old fields containing some woody vegetation. The coverage of grassland habitats in was very low (max = 5.1%) compared with studies conducted in less forested landscapes (e.g. Bakker *et al.*, 2002; max = 63%). Consequently, it is unlikely that the correlation between richness and abundance and LPC2 is a consequence of birds responding to variation in grassland cover, and more likely that birds are more likely responding to reduced tree cover associated with urbanization.

Within patch factors

Arthropod diversity and abundance have been positively linked to both increased plant (e.g. Haddad *et al.*, 2001; Gardiner *et al.* 2010; Table 2) and land cover (Weibull *et al.*, 2000) diversity. We found that more diverse plantings supported greater arthropod diversity and biomass (Table 2), but that neither metric was important in explaining richness or abundance of any subset of the avian community. The dietary importance of different foods (e.g. seed, arthropods) varies among bird species and time of year, but lepidopteran larvae are known to be particularly important in the provisioning of nestling songbirds (Van Noordwijk *et al.*, 1995). This subset of arthropod biomass was also unimportant in predicting avian abundance and richness (B. A. Robertson, unpublished results). Although food availability appears to have little direct influence on the richness and abundance of bird communities in the plantings we studied, food availability is an important selective agent shaping the reproductive strategies of birds (reviewed in Martin, 1987) and may influence avian reproductive success among biomass feedstocks.

Breeding species density and abundance in prairie and switchgrass were positively linked to increasing forb composition rather than to feedstock type, *per se* (Table 4). Because switchgrass fields were invaded to various degrees by forbs (Table 2) switchgrass and prairie plantings represented a gradient of monoculture to polyculture, rather than a dichotomy of plant composition, at least in terms of forb cover. Grassland birds have largely been categorized based upon well-understood preferences for the height and density of grasses in patches with some species preferring taller, denser habitats (e.g. Sedge Wren) and others preferring lower, more open grassland habitats (e.g. Grasshopper Sparrow). Thus, maximizing species richness in a patch requires maximizing the diversity of vegetation structure (e.g., Knopf, 1994; Herkert 1994), but evidence for this hypothesis has been mixed (Wiens, 1974; Coppedge *et al.*, 2008). In this study, we found that microhabitat heterogeneity was linked to breeding species richness in perennial plantings and competing models explaining many avian community metrics included negative relationships between richness and a quadratic component of MPC1 (MPC1^2, Fig. 3). MPC1 represents increasing values of vegetation density, standing dead vegetation and ground litter cover. Because values of MPC1^2 are centered at zero, a negative relationship with richness indicates peak richness at intermediate values of microhabitat density. These patterns are likely an indication of moderate vegetation densities being most likely to attract species preferring this habitat structure, but also some individuals of species preferring more- or less-dense habitats. These relationships largely vanished in analyses excluding corn (Table 4) suggesting the relationship may have arisen only as a consequence of generally poor species density in corn, yet MPC1^2 was still important in explaining obligate species abundance.

By sampling across plantings that varied dramatically in standing biomass and forb composition we generated predictive models of the relationship between habitat structure and composition and the response of the avian community that have implications for future bioenergy crops. Our switchgrass plantings were more structurally dense and uniform (less heterogeneous) and had a lower forb composition than prairie plantings (Table 1), generally reflective of the differences expected between agricultural monocultures and polycultures. Despite the constraints of our study, we believe that results from this analysis are useful for understanding how bird communities will respond to alternative bioenergy feedstocks and some components relevant to their eventual management regimes in the Upper Midwest.

Our results demonstrate that, in the temperate grassland region of North America, perennial feedstocks have potential to provide habitat for a greater diversity and abundance of grassland birds than traditional corn-ethanol production. The eventual industrialization of perennial bioenergy crops will aim to maximize biomass production which, especially in monocultural systems, will likely result in a uniformly tall, dense crop structure. Our findings suggest that doing so will reduce their suitability for most obligate grassland birds, generally favoring those species that tolerate denser habitat structure (e.g. Sedge Wren, Song Sparrow). New genetically improved feedstock genets along with the type and timing of chemical applications (e.g. fertilizers) and other management techniques (e.g. the timing and pattern of harvest, Murray & Best, 2003) will likely make perennial and poly-cultural biomass crops significantly different from stands found in today's landscapes that are typically managed for wildlife habitat, with unknown consequences for grassland birds and other wildlife. Ultimately, it remains too early to determine whether perennial biomass production will represent a unique conservation opportunity (Fletcher *et al*., 2010) or an important threat to the persistence of grassland birds in agricultural landscapes.

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Supporting Information

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

Table S1. Correlation matrix of microhabitat vegetation structural and composition variables.

Table S2. Eigenvalues of the first four orthogonal microhabitat principal components extracted.

Table S3. Loading matrix for the first microhabitat principal component.

Table S4. Correlation matrix of land-use categories in landscapes surrounding focal patches at the 1500 m scale.

Table S5. Eigenvalues of the first four orthogonal landscape principal components extracted.

Table S6. Loading matrix for the first two landscape principal components.

Appendix S1. Extractions of microhabitat and landscape-scale principal components of vegetation habitat structure and composition.

Appendix S2. Fit of global models for all community metrics in analyses including all planting types, and switchgrass and mixed prairie only. A value close to 1 for generalized linear models indicates good fit, while values over 4 indicate overdispersion. Goodness of fit tests for logistic regressions indicate no differences between the observed and predicted values of the dependent variables.

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