

Perennial Agroenergy Feedstocks as En Route Habitat for Spring Migratory Birds

Bruce A. Robertson · Douglas A. Landis ·
T. Scott Sillett · Elizabeth R. Loomis · Robert A. Rice

Published online: 30 September 2012
© Springer Science+Business Media New York 2012

Abstract Increased production of bioenergy crops in North America is projected to exacerbate already heavy demands upon existing agricultural landscapes with potential to impact biodiversity negatively. Grassland specialist birds are an imperilled avifauna for which perennial-based, next-generation agroenergy feedstocks may provide suitable habitat. We take a multi-scaled spatial approach to evaluate the ability of two candidate second-generation agroenergy feedstocks (switchgrass, *Panicum virgatum*, and mixed grass–forb plantings) to act as spring migratory stopover habitat for birds. In total, we detected 35 bird species in mixed grass–forb plantings and switchgrass plantings, including grassland specialists and species of state and national conservation concern (e.g., Henslow’s Sparrow, *Ammodramus henslowii*). Some evidence indicated that patches with higher arthropod food availability attracted a greater diversity of migrant bird species, but species richness, total bird abundance, and the abundance of grassland specialist species were similar in fields planted with either feedstock. Species richness per unit area (species density) was relatively higher in switchgrass fields. The percent land cover of forest in landscapes surrounding study fields was negatively associated with bird species richness and species density.

Habitat patch size and within-patch vegetation structure were unimportant in predicting the diversity or abundance of spring en route bird assemblages. Our results demonstrate that both switchgrass and mixed grass–forb plantings can attract diverse assemblages of migrant birds. As such, industrialized production of these feedstocks as agroenergy crops has the potential to provide a source of en route habitat for birds, particularly where fields are located in relatively unforested landscapes. Because industrialization of cellulosic biomass production will favor as yet unknown harvest and management regimes, predicting the ultimate value of perennial-based biomass plantings for spring migrants remains difficult.

Keywords Biofuels · Agriculture · Grassland birds · Habitat selection · Agroecology · Switchgrass

Introduction

Demand for new sources of sustainable energy has spurred interest in the production of dedicated field-grown biomass (hereafter “agroenergy”) crops. Such crops can be converted to liquid fuels via cellulosic technology or to electricity by combustion. The perceived potential for agroenergy crops to provide a significant fraction of future liquid fuel demand is sufficiently high that European and American governments have set mandated production goals [1, 2]. Such policies are projected to expand greatly the acreage of land under cultivation and intensify the management of land currently under cultivation [3]. Together, land-use change and agricultural intensification are currently regarded as the greatest current global threat to the maintenance of biodiversity and the ecosystem services it supports [4, 5]. In North America, land-use changes associated with the expansion of contemporary agroenergy crops (e.g., corn) are generally expected

B. A. Robertson · T. S. Sillett · R. A. Rice
Migratory Bird Center, Smithsonian Conservation Biology
Institute, National Zoological Park,
Washington, DC 20013, USA

B. A. Robertson (✉)
Division of Science Mathematics and Computing, Bard College,
30 Campus Drive,
Annandale-on-Hudson, NY 12504, USA
e-mail: broberts@bard.edu

B. A. Robertson · D. A. Landis · E. R. Loomis
DOE Great Lakes Bioenergy Research Center,
Michigan State University,
East Lansing, MI 48824, USA

to reduce biodiversity [6–8], yet next-generation perennial-based crops like switchgrass (*Panicum virgatum*) or mixed grass–forb combinations [9] may provide new acreage of suitable habitat for animals native to North American temperate grasslands [6, 8].

North American grassland specialist birds have experienced dramatic long-term population declines [10] and represent an important component of native biodiversity likely to be impacted by the expansion of agroenergy [6, 8, 11, 12]. Research into halting population declines has focused heavily on understanding the factors shaping the demography of breeding and wintering populations [reviewed in 13], while the migratory ecology and habitat requirements of this imperiled avifauna have received scant attention.

Migration represents a critical portion of the life cycle of temperate migratory birds because they can spend nearly one third of their life span in transit with at least one species apparently experiencing ~85 % of adult mortality during migration [14]. Recent evidence shows that switchgrass and mixed grass–forb plantings can provide en route stopover habitat for diverse bird assemblages during the fall migratory period [15]. However, the value of these fields as en route habitat during spring, when habitat structure and food availability may differ dramatically, remains unclear. As next-generation agroenergy crops are poised to transform North American agricultural landscapes, understanding their ability to provide stopover habitat for migratory birds will be central to projecting the impact of expanded production on the conservation of grassland bird populations.

Our goal is to address this information gap directly by comparing species richness, species density, and abundance of the entire migratory bird community and of grassland specialist species between two candidate agroenergy feedstocks likely to provide stopover habitat to migratory grassland birds: switchgrass and mixed grass–forb plantings. We first ask if these planting types differ in the migratory bird communities they attract during the spring migratory period, and then investigate how food availability, vegetation structure, and composition at multiple spatial scales (microhabitat, patch, and landscape) shape the distributions of spring migrant birds in fields. We base our predictions about the responses of grassland bird communities to perennial feedstocks on bird–habitat associations during the fall migratory period and in this same study system [15]. Grassland specialist species exhibit well-understood species-specific preferences for habitat structure during the breeding season [reviewed in 16] that appear to hold during the fall migratory period when species richness is similar between feedstock types and is unrelated to the biomass or diversity of arthropod food [15]. Following fall patterns, we predict that grassland specialists will avoid plantings within highly forested landscapes and prefer larger habitat patches [15] affecting overall species richness and species density. Because

the factors shaping habitat use may change seasonally, we also investigate the following factors known to shape distributions of migratory birds in other temperate North American ecosystems: food availability [reviewed in 17], habitat complexity [18], patch size [19], and the structure and composition of the surrounding landscape [20].

Methods

Study Design and Site Selection

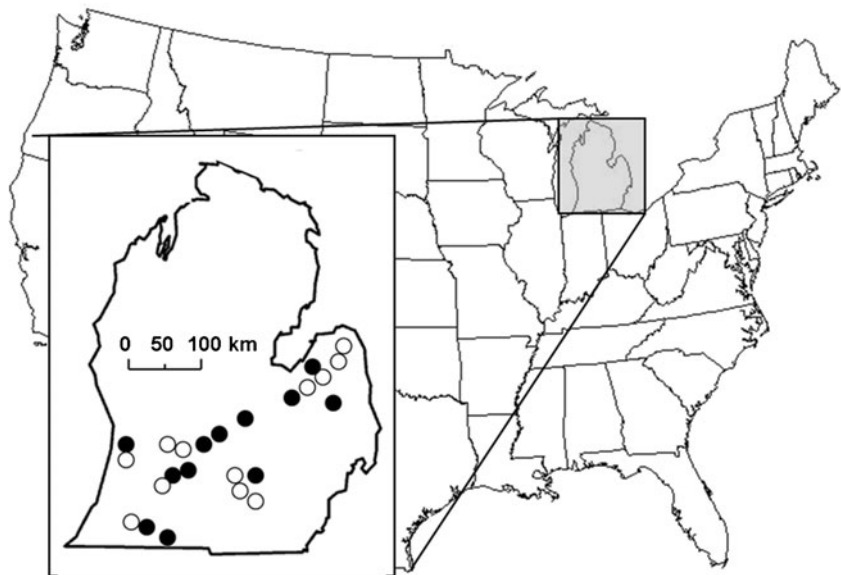
We identified established fields sown with mixed grass–forb plantings or switchgrass ($n=12$, each) throughout southern Michigan (Fig. 1). Grassland bird species specialize in habitats differing in their physical structure [16]; however, agroenergy production systems favor feedstocks and management techniques that maximize biomass, thereby reducing variation in habitat structure. Production of perennially based agroenergy feedstocks (e.g., switchgrass) by farmers or other land-managers (e.g., switchgrass) is still extremely rare throughout the Midwest, making it impossible to study crops intensively managed for biomass production. Instead, we opted to investigate vegetation structural attributes most likely to be affected by crop selection and management (e.g., harvest) and relevant to selection of en route habitat by migrant birds: (1) vegetation height and density and (2) within-field variation in structure.

In 2010, we searched for fields planted in switchgrass and mixed grass–forb plantings throughout the southern peninsula of the state of Michigan, ultimately locating 65 candidate fields. Fields were managed primarily as wildlife habitat or as native community restorations. For this reason, switchgrass fields were rarely strict monocultures. We visually inspected all candidate sites prior to the onset of research in order to assess vegetation heterogeneity. Moreover, we gathered data about the percent forest vs. row crop in a 1,500-m radius surrounding each site from previous studies [12, 15]. The two sets of information were combined in a non-mathematical fashion in order to select a set of study sites that maximized variation along these two axes. Four switchgrass fields (two of which were managed for biomass) and one mixed grass–forb planting were managed with fire during the previous fall. In order to evaluate the importance of patch size in shaping avian communities, we also selected patches to vary as widely as possible in size (mixed grass–forb, 3.2–70.8 ha; switchgrass, 2.0–36.42 ha). Study fields were located a minimum distance of 7 km from each other.

Bird Surveys

We surveyed the bird community associated with study fields in the spring of 2010, making three visits to each

Fig. 1 Map of the study region in the southern peninsula of Michigan. Locations of 12 mixed grass–forb (*filled circles*) and 12 switchgrass (*open circles*) study sites are indicated



patch: (1) April 1–8, (2) April 14–21, and (3) April 27–May 4. We conducted bird surveys during the first 3 h after sunrise. Species richness and abundance were estimated based on two survey techniques: fixed-width transects and area searches. Fixed-width transects [21] were 100 m long by 25 m wide. Because grassland birds are difficult to detect when not singing, we employed a rope drag technique in which a 25-m-long rope connecting two observers was dragged across vegetation [15]. This technique was designed to increase the detectability of grassland birds during the nonbreeding season and increase observer efficiency and bird detectability over fixed-distance point counts [22]. We identified birds visually when perched or in flight when flushed from within and aurally by species-specific calls. Individuals that could not be assigned to species were recorded as “unknown” or identified to the genus or family level (e.g., *Ammodramus* spp.). These observations were only used in estimates of community-wide abundance.

In order to obtain representative samples of bird assemblages in fields differing in area without pseudo-replicating [reviewed in 23], we varied the number of transects sampled per field, aggregating information at the patch-scale prior to any analysis. The smallest patches contained a single transect, while the number of transects surveyed per patch increased with patch size up to a maximum of six. We oriented and surveyed transects in a linear series that ran through the geographic center of each with no transect ending closer than 50 m from a patch edge. We calculated median values of species richness per transect (hereafter species density) and abundance at the patch scale, combining information from all site visits. Many grassland bird species in this region are “area-sensitive,” preferring to settle and breed in larger patches of habitat [24]. Consequently, in addition to the well-understood species-area

effect in which more species are found in larger patches [24], species richness per unit area (i.e., “species density”) increases with patch size [24]. We used species density as a metric to test the hypothesis that avian communities are also area-sensitive during the spring migratory period.

To estimate patch-scale species richness, we used area searches to survey portions of each field not covered by transects. To maintain observer effort proportional to the size of each patch, observers walked at a regular pace through each field in a systematic pattern such that one observer passed within 75 m of every point in a field exactly once. Species detected during strip-transect surveys, including those detected at a distance of >50 m, were pooled with detections from area searches to provide an estimate of total bird species richness within each patch.

Within-Patch Habitat Structure

During the second site visit, we characterized vegetation structure of perennial plantings within each transect to determine how microhabitat gradients may affect spatial distributions of birds. We randomly selected five nonoverlapping sampling points within each transect at which we recorded vertical density of vegetation and canopy coverage. Vertical density [an index of biomass, 25] was quantified by measuring the minimum height of visual obstruction from 4 m in each cardinal direction from a Robel pole at a height of 1 m [26]. We estimated canopy coverage on the basis of nonoverlapping percentages of forbs and grass using a Daubenmire quadrat viewed from 1.5 m directly above [27]. We assigned cover estimates 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 %, and 6=95–100 %) and computed mean values of microhabitat variables at the patch scale. Variation in

vegetation density within each patch was used to calculate an index of habitat heterogeneity for that patch relevant to grassland birds [28]:

$$\text{Vegetation heterogeneity index} = \frac{\sum_{i=1}^n (\text{Max } x_i - \text{Min } x_i)}{\sum_{i=1}^n \bar{x}_i}$$

Where x is the minimum height of visual obstruction on a Robel pole at of four subsamples at each sampling unit, n is the number of sampling units in each study field, of which there are $n = \#$ of transects $\times 5i$ sampling units per field.

Patch- and Landscape-Scale Variables

Grassland birds commonly avoid settling in habitat patches more extensively bordered by forest during the breeding season [reviewed in 23] and during autumn migration [15]. We estimated the percent forest composition within a 1.5-km radius surrounding study sites using ArcGIS 9.3 [29] and the 2009 Cropland Data Layer (56 m resolution) [30]. The accuracy of land-use categories was verified during site visits.

Arthropod Richness and Biomass

The distribution of migratory birds among and within patches is commonly linked to arthropod food availability [17]. We estimated the relative availability of terrestrial arthropod prey among stopover sites via sweep net samples of above-ground vegetation near the geographic center of each field during the second site visit each year. Two within-patch sweep sample transects were taken, beginning at a distance of 50 m in opposite directions from the field center on a north–south axis and consisting of 50 sweeps taken while slowly moving toward the plot center. The two within-field samples were combined and sealed in plastic bags and transferred to 90 % ethanol solution for storage. We identified individuals to the family level. We estimated individual mass using published length-regression estimates [31, 32] and computed total arthropod biomass at the patch level. Finally, we estimated patch-scale estimates of arthropod family richness using the Chao 2 asymptotic richness estimators in the program EstimateS [33].

Statistical Analysis

We used a multi-model inference approach to determine the relative importance and effect size of seven environmental variables and feedstock type (Table 2) in explaining variation in (1) the community-wide species richness and (2) species density, (3) total bird abundance, and (4) abundance of grassland specialist/obligate bird species [*sensu* 34], (see Table 1). Because birds may weigh microhabitat structure,

patch size, and land cover composition simultaneously in making settlement decisions, we consider potential interactions between feedstock and patch size, and feedstock and forest cover in predicting avian diversity and abundance metrics. We log transformed patch size prior to analysis because species richness generally increases with patch size in an asymptotic and nonlinear fashion [35]. Vegetation density was square root transformed to achieve normality.

Because avian community variables followed Poisson distributions typical of count data, and were overdispersed, we modeled arthropod community variables using either negative binomial or quasi-Poisson regression with a log link function [36]. We began by entering all independent variables and the above-mentioned interaction terms into a full generalized linear model. Next, all possible subsets of the that model were analyzed using the multimodel inference package, MuMin in R v. 2.11.1 [37]. We used MuMin to estimate model coefficients and bias-corrected quasi-AIC_c values, an adaptation of Akaike's Information Criterion (AIC) that accounts for potential overdispersion in count data and contains a small sample size adjustment [38]. We used differences between the QAIC_c-best model and other candidate models (ΔQAIC_c) to calculate Akaike weights (ω_+) for each candidate. We then summed the weights of ranked models 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 associated with study sites in explaining avian community metrics (Table 3). A full discussion of the information-theoretic approach to model/variable selection used here can be found in [36].

Because study fields in closer physical proximity may have similar characteristics, we computed the Moran's I test for residual spatial autocorrelation (60 km distance band) for the best models using the spatial dependence package, *spdep* in R [39]. We found no evidence of autocorrelation ($0.08 > I > 0.03$; $P > 0.32$ for all tests).

Results

Bird and Arthropod Community Composition

We identified 97.4 % of the 301 individuals detected within transects to the species level. In total, we detected 35 bird species, with equal total species richness in both feedstocks ($n=20$) and similar obligate species richness in each

Table 1 Bird species ($n=36$) detected in during spring migration within mixed grass–forb and switchgrass fields ($n=12$, each) in southern Michigan

Species	Switchgrass	Mixed grass–forb
American Goldfinch (<i>Spinus tristis</i>)	X	X
American Kestrel (<i>Falco sparverius</i>)		X
American Robin (<i>Turdus migratorius</i>)	X	X
Barn Swallow (<i>Hirundo rustica</i>)	X	X
Brown-headed Cowbird (<i>Molothrus ater</i>)	X	X
Bobolink (<i>Dolichonyx oryzivorus</i>)^a	X	X
Clay-colored Sparrow (<i>Spizella pallida</i>)	X	X
Chipping Sparrow (<i>Spizella passerina</i>)	X	X
Common Grackle (<i>Quiscalus quiscula</i>)	X	X
Common Yellowthroat (<i>Geothlypis trichas</i>)	X	X
Eastern Bluebird (<i>Sialia sialis</i>)	X	X
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	X	X
Eastern Meadowlark (<i>Sturnell magna</i>)^a	X	X
European Starling (<i>Sturnus vulgaris</i>)		X
Field Sparrow (<i>Spizella pusilla</i>)	X	X
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)^{a, b}	X	X
Henslow's Sparrow (<i>Ammodramus henslowii</i>)^{a,c,d}		X
Horned Lark (<i>Eremophila alpestris</i>)		X
Killdeer (<i>Charadrius vociferus</i>)	X	
Mallard (<i>Anas platyrhynchos</i>)	X	X
Mourning Dove (<i>Zenaidura macroura</i>)	X	
Northern Flicker (<i>Colaptes auratus</i>)	X	X
Northern Harrier (<i>Circus cyaneus</i>) ^{a,b}	X	
Ring-necked Pheasant (<i>Phasianus cholchicus</i>)	X	X
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	X	X
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	X	X
Savannah Sparrow (<i>Passerculus sandwichensis</i>)^a	X	X
Sedge Wren (<i>Cistothorus platensis</i>)^a	X	X
Song Sparrow (<i>Melospiza melodia</i>)	X	X
Swamp Sparrow (<i>Melospiza georgiana</i>)	X	X
Tree Swallow (<i>Tachycineta bicolor</i>)	X	X
Turkey Vulture (<i>Cathartes aura</i>)	X	X
Unknown sparrow spp.	X	
<i>Spizella</i> sparrow spp.	X	
Vesper Sparrow (<i>Pooecetes gramineus</i>) ^a	X	X
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	X	
Wilson's Snipe (<i>Gallinago delicata</i>)	X	X
Yellow Warbler (<i>Dendroica petechia</i>)		X
Totals	33 (5)	33 (6)

Species totals in parentheses represent obligate grassland species on April 1–May 4, 2010. Species names in bold and species totals in parentheses represent those for which published research indicates they breed exclusively within grassland habitats

^a Obligate grassland species

^b Michigan species of concern

^c Michigan endangered species

^d Species appearing on the Audubon watchlist (National Audubon Society 2007) [58]

Table 2 Comparisons of seven explanatory variables and avian community metrics between mixed grass–forb ($n=12$) and switchgrass fields ($n=12$) in southern Michigan

Variable	Mixed grass–forb	Switchgrass	t_{22}	P
Within-patch				
Microhabitat heterogeneity index (0–2)	1.03 (0.13)	1.00 (0.17)	0.16	0.55
Mean minimum height of Robel pole intercept (cm)	20.0 (2.3)	41.1 (7.1)	2.83	0.01
Mean ground cover index broad-leaved plants (1–6)	1.5 (0.2)	1.3 (0.2)	0.75	0.46
Arthropod biomass (mg/sample)	2.43 (0.80)	0.67 (0.27)	2.07	0.05
Arthropod richness (# families)	11.4 (3.1)	5.1 (1.8)	1.70	0.10
Patch and landscape scale				
Patch size (ha)	16.4 (5.4)	7.6 (2.7)	1.45	0.16
Surrounding land cover in forest (1.5-km radius) (%)	31.0 (0.1)	31.0 (0.1)	0.15	0.98
Avian community metrics				
Species richness	8.6 (0.7)	6.9 (1.1)	1.27	0.22
Species density (species/ha)	6.6 (1.6)	12.2 (2.0)	1.60	0.13
Community-wide abundance	3.5 (0.8)	0.5 (0.2)	1.55	0.13
Obligate grassland species abundance	1.1 (0.4)	0.5 (0.2)	1.32	0.20

Mean values and standard errors (SE) are given for parameter estimates along with critical and P values of independent samples t tests

planting type (switchgrass=5, mixed grass–forb=6, Table 1). Several species of high state and national conservation status (e.g., Grasshopper Sparrow, Henslow’s Sparrow, and Northern Harrier) were detected. We identified 222 arthropods from 101 families. Terrestrial arthropod biomass was greater in mixed grass–forb plantings, but richness was similar between feedstocks (Table 2).

Vegetation Structure, Patch Size, and Land Cover

Study fields varied in size from 2.0 to 70.8 ha. Microhabitat heterogeneity, vegetation density, percent forest cover surrounding study fields, and the size of study fields did not differ between switchgrass and mixed grass plantings (Table 2). On average, the percentage of ground cover in

Table 3 Parameter estimates ($\beta \pm$ unconditional SE) from the QAIC_c-best model predicting the (1) species richness, (2) species density, (3) abundance of all birds, and (4) abundance of obligate grassland bird

species exploiting switchgrass and mixed grass–forb plantings as spring migratory stopover habitat in southern Michigan

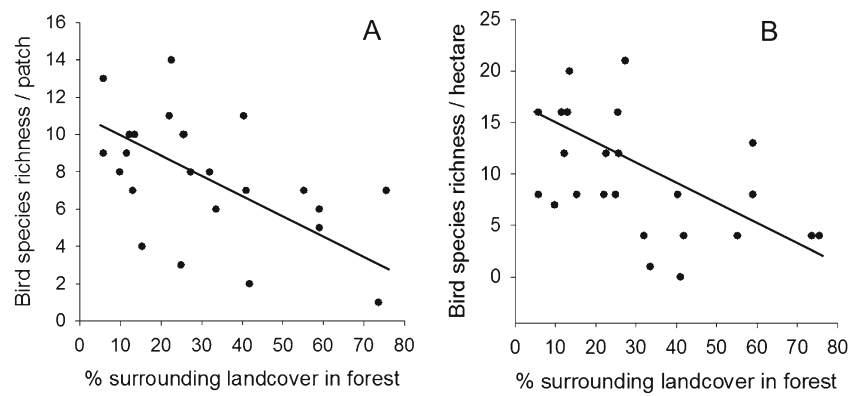
Parameter	Species richness		Species density		Total abundance		Obligate abundance	
	β (SE)	$\omega+$	β (SE)	$\omega+$	β (SE)	$\omega+$	β (SE)	$\omega+$
Intercept	1.97 (0.42)***		1.11 (0.50)***		1.46 (0.45)***		0.07 (0.96)	
Feedstock ^a		0.21	2.00 (0.28)*	0.44		0.13		0.27
Habitat heterogeneity		0.18		0.17		0.14		0.15
Forb cover		0.44		0.16		0.14		0.29
Arthropod biomass (mg/sample)	16.80 (24.8)**	0.38		0.15		0.14		0.12
Arthropod richness (families/sample)		0.37		0.14		0.13		0.14
Vegetation density (ht. of pole intcpt, cm)		0.13		0.23		0.13		0.13
Log patch size (ha)		0.25		0.28		0.15		0.14
% forest cover (1.5-km radius)	-0.87 (0.64)***	0.76	-1.31 (0.91)*	0.81		0.14		0.43
Feedstock \times Log patch size		0.03		0.04		0.13		0.03
Feedstock \times % forest cover		0.00		0.02		0.13		0.02

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 ω 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 the experiment. Blank spaces indicated a parameter was not included in the QAIC_c-best model

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

^a Mixed grass–forb was the reference category

Fig. 2 Partial regressions of bird species richness vs. percent forest cover surrounding plantings (1.5-km radius) (a), and bird species density (species richness/hectare) vs. percent forest cover surrounding plantings (1.5-km radius) (b). Parameter estimates are based on model-averaged values



broad-leaved plants was low, averaging between 5 and 25 % in both planting types.

Avian Community Metrics

Avian species richness was primarily affected by forest cover and arthropod biomass (Table 3). The QAIC_c-best model ($\hat{c}=1.52$) predicted a significant increase in richness in patches with higher arthropod biomass and in landscapes with lower forest cover (Fig. 2a). Higher bird species richness was also associated with greater terrestrial arthropod biomass. Forest cover received strong support across the entire model set ($\omega_+=0.76$) indicating this variable was consistently included in the most predictive models. Support for arthropod biomass and other variables was generally lower ($\omega_+\leq 0.44$; Table 3), suggesting they were less likely to be included in the model in repeated runs of the experiment.

Species density was affected by feedstock type and forest cover. The QAIC_c-best model ($\hat{c}=1.17$) predicted roughly 100 % increase in species density in switchgrass fields compared mixed grass–forb plantings (Tables 2 and 3). Patches with an increasing percentage of forest cover surrounding them exhibited decreasing species density (Fig. 2b). These effects were moderately to strongly supported (percent forest cover, $\omega_+=0.81$; feedstock, $\omega_+=0.64$) compared to other predictors ($\omega_+\leq 0.23$; Table 3).

Global models predicting total bird abundance and that of obligate grassland species fit the data reasonably well (total abundance, $\hat{c}=2.43$; obligate abundance, $\hat{c}=1.14$), but QAIC_c-best models for each analyses contained only the intercept. Support for the importance of predictor variables and interactions were poor for all variables across both model sets and for both abundance measures ($\omega_+\leq 0.33$; Table 3). Support for models including interactions between feedstock type and either patch size or forest cover were extremely poor ($\omega_+\leq 0.13$; Table 3) across models sets for all for avian community metrics we examined.

Discussion

This study represents one of the first to assess the relative biodiversity value of alternative next-generation agroenergy feedstocks in North America empirically [also see 12, 15, 40], and is the first to investigate the habitat associations of grassland birds during spring migration. Most studies investigating how birds select migratory stopover habitat have focused efforts at a single small spatial scale [20], and research has taken place almost exclusively within forested ecosystems. We simultaneously compared the influence of factors operating at different spatial scales [see also 20, 41], focusing our efforts on the entire migratory bird community and on grassland specialists to understand better how factors intrinsic and extrinsic to agroenergy plantings may more broadly affect the ability of agricultural landscapes to act as migratory stopover habitat. We found some support for the contention that switchgrass and mixed grass–forb feedstocks differ in their suitability as en route habitat during spring. However, habitat composition at the landscape scale appeared to be more broadly important than differences among feedstocks in attracting diverse bird assemblages to agroenergy feedstocks during spring migratory movements.

We detected bird species of state and continental conservation concern in fields planted with both feedstock types. The total number of bird species detected in switchgrass and mixed grass–forb plantings was identical, and the number of obligate grassland bird species detected was similar. Results from our multi-model inference analysis indicate that switchgrass fields supported greater species density (species richness per unit area), but that bird species richness in switchgrass fields was similar to that of mixed grass–forb plantings.

Vegetation heterogeneity in switchgrass and mixed grass–forb plantings was similar, but switchgrass fields had greater average vegetation density than mixed grass–forb fields. This difference in average vegetation density between feedstock types, however, was not linked to the elevated species density we identified in switchgrass fields. These results contrast with bird–microhabitat relationships identified during the fall migratory period in this study

system in which vegetation structural heterogeneity was the single most important within-patch factor shaping both bird community composition and abundance [15].

Seasonal differences in habitat structure may explain these apparently conflicting results. For example, habitat heterogeneity is commonly associated with species richness of fall migrants in forested systems [e.g., 18, 19, 42–44], and may be particularly important in attracting species with a range of habitat structural preferences to grasslands during fall when within-field heterogeneity is relatively low (fall = 0.35, SD = 0.18; spring = 1.0, SD = 0.53) [this study, and 15 with comparable methodology]. Though seasonal changes in habitat use at the species and community level have been noted in temperate forested systems [42, 45–47], they have not been explicitly linked to variation in microhabitat structure. This lack of a consistent between-season relationship between bird diversity and feedstock vegetation characteristics might result from the cumulative effects of variable species-specific responses to habitat structure [48]. Alternatively, it could reflect the region- or habitat-specific dependence of habitat structure in mediating (1) availability of or accessibility to food [49], (2) resource competition within or between species [50], or (3) risk of predation [51].

When selecting breeding habitat, many grassland specialists avoid habitat patches within highly forested landscapes [49, 52], and this forest avoidance may be a mechanism shaping area sensitivity in breeding grassland specialist birds [23]. In addition, the richness of en route migratory bird assemblages has been known to increase with patch size in forested [19, 50] and grassland habitats [15]. In this study, forest cover (1.5-km radius scale) was the single most important factor we identified in predicting reduced species richness and species density in both feedstock types, independently of patch size. This indicates that a significant portion of the avian species assemblage that exploits feedstock plantings exhibits forest avoidance behavior in selecting patches of stopover habitat during spring migration, and that patch size per se is relatively unimportant.

This result is somewhat surprising given that these same bird community metrics were not linked to forest avoidance in Robertson et al.'s [15] study conducted in this system during the fall migratory period. In that study, some individual birds detected in mixed grass–forb and switchgrass plantings were likely remaining in their natal habitat patches and staging for migration. Consequently, the inclusion of post-breeding individuals in models of fall migratory bird assemblages may have confused the abundance of individuals associated with particular breeding habitats with the attractiveness of these patches for migrants. Even so, this does not negate the potential importance of mixed grass–forb and switchgrass habitats for post-breeding individuals staging for migration. It does potentially confound factors shaping the distribution of these individuals from that of

those stopping over during the migratory journey. In contrast, the present study was conducted during a time period when the only non-migrant bird species present should be a low abundance of a few overwintering resident species (mostly Song Sparrows and American Goldfinches) [53]. Collectively, and consistent with the results of studies of this system during other time periods [12, 15], our results imply that cultivation of perennial-based agroenergy crops in less forested landscapes will attract a greater diversity of migratory bird species. Moreover, it appears that en route grassland specialist species will benefit more from this crop placement strategy during the fall [15] than spring migratory period.

Spatial variation in the biomass or diversity of arthropod prey is commonly associated with the distribution of migrating birds [reviewed in [18, 20, 48]]. This is not surprising given the energetic demands of migration and the need to rapidly refuel [54]. We found weak evidence that bird species richness was positively related to arthropod food availability, paralleling a similar relationship during the fall migratory period in this system [15]. We captured 40 times fewer individual arthropods per patch than Robertson et al. [15] did during the fall migratory period in this system, representing a marginal mean biomass roughly six times smaller (mixed grass–forb comparison only, spring = 2.4 mg, SD = 2.7; fall = 15.1 mg, SD = 12.0). Yet, variation in arthropod biomass during the fall migratory period was not linked to distributions of migrants [15]. Again, potential relationships may have been obscured by the combining observations of post-breeding and actively migrating individuals in that study. Alternatively, birds may more closely track the distributions of arthropods during spring when that food source is rarer. Seeds, too, may represent an important caloric resource important to many grassland migrants whose distribution could influence settlement decisions during spring migration, but that we did not examine in this study.

We draw inferences from bird–habitat relationships based on extant variation in within-patch habitat structure, yet most of the switchgrass and mixed grass–forb fields we studied were not actively managed for agrofuel production. Moreover, we have not investigated how the migratory birds' assemblages associated with perennially based feedstocks compare with those of contemporary agrofuel crops like corn, or if birds use corn fields in spring at all. In addition to the implementation of more intensive cultivation methods, industrialization of perennially based agroenergy crops will likely include chemical applications and the selection of high-biomass genotypes that have potential to reduce plant species diversity [55] and structural heterogeneity, especially in monocultural systems. Consequently, the bird–habitat relationships we have identified can best be considered as useful in informing best farming practices and suggesting management tools in the development of sustainable agroenergy production systems.

More research is needed in order to properly evaluate the full potential of perennially based crops to act as en route habitat for grassland birds in the USA. Because most fields we studied were not harvested for biomass during the previous fall, over-winter matting of standing grass and forbs may cause delayed spring vegetation growth compared to pastures and other adjacent habitat. Moreover, if spring migrant use of perennial crops is limited by a lack of food availability or vegetation structure as it is in annual crops [56], the timing of fall harvest may have a profound impact on spring migrant use of fields. For this reason, harvest strategies (e.g., partial or staggered harvest) that have the effect of increasing spring re-vegetation rate or enhancing within- or between-field structural diversity during the migratory period could be a management tool for increasing avian biodiversity at one or more spatial scales [15, 57] and in both fall and spring. Collectively, the impact of harvesting perennial agro-energy feedstocks on migratory grassland birds remains unclear and is an important focus for future research.

We conclude that candidate next-generation perennial agroenergy feedstocks have potential to act as spring migratory stopover habitat for a significant assemblage of habitat generalist and grassland specialist birds, especially if producers can be encouraged to locate plantings within relatively unforested regions. While our results indicate some differences in the species richness of birds stopping over in mixed grass–forb and switchgrass plantings, the largely similar en route land bird assemblages in these two planting types suggest no clear advantage of one feedstock vs. the other in attracting a diversity or abundance of migrant birds. In the end, perennial feedstocks may represent an important conservation opportunity for grassland birds, but the realization of any such potential appears highly dependent upon the development and implementation of crop management strategies that enhance the suitability of fields to grassland birds and whether such management is economically sustainable.

Acknowledgments This work was funded by the Migratory Bird Center of the Smithsonian Conservation Biology Institute, US Fish and Wildlife Service (grant # 30181AG045), the DOE Great Lakes Bioenergy Research Center (DOE BER Office of Science DE-FC02-07ER64494), DOE OBP Office of Energy Efficiency and Renewable Energy (DE-AC05-76RL01830), and the U.S. National Science Foundation LTER program.

References

- European Union (2009) Directive 2009/28/EC of the European Parliament and of the Council of 23 April, 2009 on the promotion of the use of energy from renewable sources and amending and subsequently repealing directives 2001/77/EC and 2003/30/EC
- US Congress (2007) Energy Independence and Security Act of 2007. Renewable fuels directive. <http://www.govtrack.us/congress/billtext.xpd?bill=h110-6>. Accessed 26 May 2009
- West T, Dunphy-Guzman K, Sun A, Malczynski L, Reichmuth D, Larson R et al (2009) Feasibility, economics, and environmental impact of producing 90 billion gallons of ethanol per year by 2030. Sandia National Laboratories, Livermore
- Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. *Science* 307:550–555
- Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC
- Fargione JE, Cooper TR, Flaspohler DJ, Hill J, Lehman C, McCoy T et al (2009) Bioenergy and wildlife: threats and opportunities for grassland conservation. *Bioscience* 59:767–777
- Meehan TD, Hurlbert AH, Gratton C (2010) Bird communities in future bioenergy landscapes of the Upper Midwest. *PNAS* 107:18533–18538
- Fletcher RJ, Robertson BA, Evans J, Doran P, Alavalapati JRR, Schemske D (2011) Biodiversity conservation in the era of bio-fuels: risks and opportunities. *Front Ecol Env* 9:161–168
- Tilman D, Hill J, Lehman C (2006) Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science* 314:1598–1600
- Sauer JR, Hines JE, Fallon J (2008) The North American breeding bird survey, results and analysis 1966–2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel
- Scharlemann JPW (2008) Can bird research clarify the biodiversity benefits and drawbacks of biofuels? *Ibis* 150:640–642
- Robertson BA, Doran P, Robertson R, Loomis L, Schemske D (2011) Perennial biomass feedstocks enhance avian diversity. *GCB Bioenergy* 3:235–246
- Askins RA, Chavez-Ramirez F, Dale BC, Haas CA, Herkert JA (2007) Conservation of grassland birds in North America: understanding ecological processes in different regions. *Ornithol Monogr* 124:1–46
- Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* 71:296–308
- Robertson BA, Robertson JR, Loomis ER, Doran JP, Schemske DW (2011) Avian use of perennial biomass feedstocks as post-breeding and migratory stopover habitat. *PLoS One* 6(3):E16941
- Sample DW, Mossman MJ (1997) Management of habitat for grassland birds: a guide for Wisconsin. Wisconsin Department of Natural Resources, Madison
- Moore FR, Gauthreaux SAJ, Kerlinger P, Simons TR (1995) Habitat requirements during migration: important link in conservation. In: Martin TE, Finch DM (eds) Ecology and management of neotropical migratory birds. Oxford University Press, Oxford, pp 121–144
- Rodewald PG, Brittingham MC (2004) Stopover habitats of land-birds during fall: use of edge-dominated and early-successional forests. *Auk* 121:1040–1055
- Martin TE (1980) Diversity and abundance of spring migratory birds using habitat islands on the Great Plains. *Condor* 82:430–439
- Buler JJ, Moore FR, Norris K (2007) A multi-scale examination of stopover habitat use by birds. *Ecology* 88:1789–1802
- Emlen JT (1977) Estimating breeding season bird densities from transect counts. *Auk* 94:455–468
- Fletcher RJ, Dhundale JA, Dean TF (2000) Estimating non-breeding season bird abundance in prairies: a comparison of two survey techniques. *J Field Ornith* 71:321–329
- Ribic CA, Koford R, Herkert JR, Johnson DH, Niemuth ND, Naugle DE et al (2009) Area sensitivity in North American grassland birds: patterns and processes. *Auk* 126:233–244
- Herkert JR (1994) The effects of habitat fragmentation on Mid-western grassland bird communities. *Ecol Appl* 4:461–471
- Harmoney KR, Moore KJ, George R, Brummer EC, Russell JR (1997) Determination of pasture biomass using four indirect methods. *Agron J* 89:665–672

26. Robel RJ, Briggs JA, Dwyer D, Hulbert DL (1970) Relationships between visual obstruction measurements and weight of grassland vegetation. *J Range Manage* 23:295–297
27. Daubenmire R (1959) A canopy-coverage method of vegetation analysis. *Northwest Sci* 33:43–64
28. Weins JA (1974) Habitat heterogeneity and avian community structure in North American grasslands. *Am Midl Nat* 91:195–213
29. ESRI (2008) ArcGIS. ESRI, Redlands
30. United States Department of Agriculture (2010) 2009 Cropland data layer. National Agricultural Statistics Service, Washington, D.C
31. Rogers LE, Hinds WT, Buschbom RL (1976) A general weight vs. length relationship for insects. *Ann Ent Soc Am* 69:387–389
32. Hódar JA (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Ecol* 17:421–433
33. Colwell RK (1997) EstimateS: statistical estimation of species richness and shared species from samples. Version 5. User's guide and application. Available: <http://viceroy.eeb.uconn.edu/estimates>. Accessed 27 July 2010
34. Vickery PD, Tubaro PL, Dasilva JMC, Peterjohn BG, Herkert JR, Cavalcanti RB (1999) Conservation of grassland birds in the Western Hemisphere. In: Vickery PD, Herkert JR (eds) *Ecology and conservation of grassland birds of the Western Hemisphere*. Stud Avian Biol 19. Cooper Ornithological Society, Camarillo, pp 2–26
35. Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge
36. Burnham KP, Anderson DR (2002) *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd edn. Springer, New York
37. R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. Version 2.12.1. ISBN 3-900051-12-7. <http://www.R-project.org>. Accessed 9 March 2012
38. Legendre P, Vaudor A (1991) *The R Package: Multidimensional analysis, spatial analysis*. Department of Biological Sciences, University of Montréal, Montréal
39. Bivand R, Altman M, Anselin L et al. (2010) Package 'spdep', R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>. Accessed 15 Nov 2010
40. Gardiner MA, Tuell JK, Isaacs R, Gibbs J, Ascher JS, Landis DA (2010) Implications of three model biofuel crops for beneficial arthropods in agricultural landscapes. *Bioenergy Res* 3:6–9
41. Deppe JL, Rotenberry JT (2008) Scale-dependent habitat use by fall migratory birds: vegetation structure, floristics, and geography. *Ecol Monogr* 78:461–487
42. Hutto RL (1985) Seasonal changes in the habitat distribution of transient insectivorous birds in south eastern Arizona: competition mediated? *Auk* 102:120–132
43. Moore FR, Kerlinger P, Simons TR (1990) Stopover on a Gulf coast barrier island by spring trans-Gulf migrants. *Wilson Bull* 102:487–500
44. Champlin TB, Kilgo JC, Moorman CE (2009) Food abundance does not determine bird use of early-successional habitat. *Ecology* 90:1586–1594
45. Blake JG (1984) A seasonal analysis of bird communities in southern Nevada. *Southwest Nat* 29:463–474
46. Dinsmore JJ, Kent TH, Koenig D, Peterson PC, Roosa DM (1984) Iowa birds. Iowa State University Press, Ames
47. Farley GH, Ellis LM, Stuart JN, Scorr NJ (1994) Avian species richness in different aged stands of riparian forest along the middle Rio Grande, New Mexico. *Cons Biol* 8:1098–1108
48. Petit DR (2000) Habitat use by landbirds along Neartic–Neotropical migration routes: implications for conservation of stopover habitats. *Stud Avian Biol* 20:15–33
49. Ribic CA, Sample DW (2001) Associations of grassland birds with landscape factors in southern Wisconsin. *Am Midl Nat* 146:105–121
50. Moore FR, Yong W (1991) Evidence of food based competition among passerine migrants during stopover. *Behav Ecol Sociobiol* 28:85–90
51. Cimprich DA, Woodrey MS, Moore FR (2005) Passerine migrants respond to variation in predation risk during stopover. *Anim Behav* 69:1173–1197
52. Bakker KK, Naugle DE, Higgins KF (2002) Incorporating landscape attributes into models for migratory grassland bird conservation. *Cons Biol* 16:1638–1646
53. Chartier AT, Ziamo J (2004) *A birders guide to Michigan*. American Birding Association, Colorado Springs
54. Berthold P, Terrill SB (1991) Recent advances in studies of bird migration. *Ann Rev Ecol Syst* 22:357–378
55. Adler PR, Sanderson MA, Weimer PJ, Vogel KP (2009) Plant species composition and biofuel yields of conservation grasslands. *Ecol Appl* 19:2202–2209
56. Galle AM, Linz GM, Homan JH, Bleier WJ (2009) Avian use of harvested crop fields in North Dakota during spring. *West N Am Nat* 69:491–500
57. Roth AM, Sample DW, Ribic CA, Paine L, Undersander DJ, Bartelt GA (2005) Grassland bird response to harvesting switchgrass as a biomass energy crop. *Biomass Bioenergy* 28:490–498
58. National Audubon Society (2007) Audubon watchlist. <http://web1.audubon.org/science/species/watchlist>. Accessed 7 Jan 2009