

Birds and butterflies respond to soil-induced habitat heterogeneity in experimental plantings of tallgrass prairie species managed as agroenergy crops in Iowa, USA

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Summary

1. The maintenance of habitat heterogeneity in agricultural landscapes has been promoted as a key strategy to conserve biodiversity. Animal response to grassland heterogeneity resulting from spatiotemporal variation in disturbance is well documented; however, the degree to which edaphic variation generates heterogeneity detectable by grassland wildlife has proven more difficult to study in natural settings.

2. We conducted a field experiment to study how soils directly affect vegetation structure and composition and indirectly affect bird and butterfly assemblages using plantings of tallgrass prairie species managed as agroenergy crops in Iowa, USA. The experimental design included four vegetation treatments of varying species richness replicated on three soil types.

3. Habitat characteristics varied widely among soils. Crops on sandy loam, the driest, most acidic soil with the lowest nutrient content, developed shorter, less dense vegetation with sparse litter accumulation and more bare ground compared to crops on loam and clay loam.

4. Birds and butterflies responded similarly to soil-induced variation in habitat characteristics. Their abundance and species richness were similar on all soils, but their assemblage compositions varied among soils in certain vegetation treatments.

5. In low-diversity grass crops, bird assemblages using sandy loam were dominated by species preferring open ground and sparse vegetation for foraging and nesting, whereas assemblages using loam and clay loam were dominated by birds preferring tall, dense vegetation with abundant litter. In high-diversity prairie crops, the species composition of forbs in bloom varied among soils and strongly influenced butterfly assemblages.

6. *Synthesis and applications.* Prairie agroenergy crops established with identical management practices developed variable habitat characteristics due to natural edaphic variation, and this heterogeneity influenced the spatial distribution of bird and butterfly assemblages due to differential habitat use among species. This finding suggests that if unfertilized prairie crops were grown for agroenergy by land managers large-scale, soil-induced habitat heterogeneity would promote wildlife diversity within and among fields, further increasing the habitat value of these crops compared to the fertilized, annual monocultures that currently dominate the agricultural landscape. Our study also highlights the need for managers to consider soil properties when selecting sites to restore grassland habitat for species of conservation concern.

Key-words: agricultural biodiversity, avian ecology, biofuel, community ecology, disturbance, edaphic variation, grassland restoration, habitat use, Lepidoptera, soil ecology

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Introduction

The positive association between habitat heterogeneity and species diversity has been well documented for many taxa at various spatiotemporal scales (MacArthur & Wilson 1967; Tews *et al.* 2004). Areas encompassing structurally complex habitats may support greater species diversity through increased partitioning of available niche space and subsequent reductions in interspecific competition or by providing access to unique resources, predator-free refugia, or keystone structures in habitat mosaics (Law & Dickman 1998; Tews *et al.* 2004; Cramer & Willig 2005; Bennett, Radford & Haslem 2006). In agricultural landscapes, the intensification of production systems and homogenization of land management over the past century have driven the loss of habitat heterogeneity at multiple spatiotemporal scales, causing widespread biodiversity loss (Benton, Vickery & Wilson 2003). For example, in North America's tallgrass prairie region, the transition from small, diverse farms cultivating heterogeneous mixtures of annual row crops and perennial sod crops for livestock to larger farms producing corn *Zea mays* and soybean *Glycine max* monocultures (Jackson 2002) has homogenized the agricultural landscape and resulted in widespread reduction in the extent and heterogeneity of grassland habitats (Samson & Knopf 1994), with consequent declines in bird (Sauer & Link 2011) and butterfly (Swengel *et al.* 2011) biodiversity.

Bird and butterfly habitat selection are multiscale processes influenced by landscape composition, large-scale variation in macrohabitat or cover types, and fine-scale variation in microhabitat characteristics (Block & Brennan 1993; Renfrew & Ribic 2008; Mayor *et al.* 2009). In agricultural landscapes of the tallgrass prairie region, large-scale patterns of macrohabitat variation and landscape composition determine the set of birds and butterflies from the regional species pool that occupy perennial grassland habitats at the field scale (Cunningham & Johnson 2006; Davis, Debinski & Danielson 2007). Once the local species set is established, patch-level variation in vegetation structure and composition may influence home range or territory placement within fields, as well as the distribution of individuals' foraging, sheltering, displaying, and nesting or ovipositing locations within their home range (Wiens 1974; Block & Brennan 1993).

Habitat heterogeneity in tallgrass prairies is generated by variation in vegetation structure and/or plant community composition. Heterogeneity often arises when the extent and frequency of local disturbances, especially fire and grazing, vary in space and time (Glenn, Collins & Gibson 1992). Numerous studies in the tallgrass prairie region have investigated the degree to which land management practices employing fire and/or grazing generate habitat heterogeneity and how animal communities are structured in response to these management actions (Fuhlendorf & Engle 2004; Fuhlendorf *et al.* 2006). Habitat heterogeneity may also arise when local disturbance

regimes are identical if spatial variation in topo-edaphic characteristics causes differential plant establishment and/or growth over time (Benton, Vickery & Wilson 2003). Past studies have demonstrated that heterogeneity in soil nutrient resources can influence the productivity and diversity of recently established tallgrass prairies (Baer *et al.* 2003, 2005). Animal response to this source of heterogeneity has proven more difficult to study in natural settings due to the great number of potential confounding variables, including landscape and legacy effects. However, in restored prairies on heterogeneous soils, spatial variation in vegetation structure and composition among soil types might be expected to influence fine-scale bird and butterfly distribution and microhabitat use. For example, individuals might select areas with taller, denser vegetation to provide concealment from predators or cover from wind or thermal extremes, whereas areas with more bare ground, patchier vegetation, and/or emergent forbs may be used for basking or displaying to conspecifics (Wiens 1974; Fisher & Davis 2010). Heterogeneity among soils may also affect the abundance, diversity and accessibility of food resources (Wilson, Whittingham & Bradbury 2005), including seeds and arthropods for birds and host plants or nectar sources for butterflies. However, we are unaware of published studies that have experimentally manipulated plant communities on multiple soil types at scales large enough to influence animal habitat use, or, consequently, to document the indirect, vegetation-mediated effects of soils on the spatial distribution of higher trophic levels.

We sought to address this gap in the literature by conducting a field experiment to study how soils directly affect vegetation and indirectly affect bird and butterfly assemblages in plantings of tallgrass prairie species managed as agroenergy crops in Iowa, USA. The experiment converted annual row crop fields to an experimental mosaic of four perennial agroenergy crops replicated on three soil types with varying physical and chemical properties. We predicted that vegetation established with identical management practices on different soils would develop variable habitat characteristics due to differential plant establishment and growth, and we conducted repeated, fine-scale surveys of birds and butterflies using the plots to determine whether habitat heterogeneity among soils resulted in differences in observed use by bird and butterfly assemblages via habitat selection. We recognize that the small, within-field plots we surveyed do not support stable communities of birds or butterflies and that at broader spatiotemporal scales, all individuals recorded in our study belong to the same ecological community. Ecologists must always define the spatiotemporal bounds of communities under study, and here we use the term 'assemblage' simply to refer to the taxonomically related subset of the local species pool that used each plot for foraging, sheltering, and/or breeding during our study.

Birds and butterflies evolved in dynamic grassland ecosystems where suitable habitat patches moved in a

shifting mosaic in response to spatial variation in topographic characteristics and spatiotemporal variation in local disturbance events (Fuhlendorf *et al.* 2006; Swengel *et al.* 2011). Both are vagile, readily colonize restored grasslands, and have well-documented habitat preferences (Johnson, Igl & Dechant Shaffer 2004; Davis, Debinski & Danielson 2007). For these reasons, we believed these taxa would respond rapidly to the transition from annual to perennial agroenergy crops at our site.

Materials and methods

STUDY DESIGN AND SITE MANAGEMENT

We conducted our research at the Cedar River Natural Resource Area in Black Hawk County, Iowa, USA (42°23'N, 92°13'W). The experiment converted seven agricultural fields (4.0–6.4 ha) with a >20-year history of corn and soybean cultivation to four mixes of perennial tallgrass prairie plants in 48 research plots (0.30–0.56 ha) replicated on three soil types: (i) Flagler sandy loam (henceforth, 'sandy loam'), (ii) Waukee loam ('loam') and (iii) Spillville–Coland complex ('clay loam') (Table 1). Plots were scaled to maximize area (clay loam, \bar{x} = 0.55 ha; sandy loam, 0.39 ha; loam, 0.31 ha) while fitting within the largest patches of homogenous soils in the study area.

To ensure uniform management prior to seeding, fields were sprayed with glyphosate to control weeds and planted to Roundup® Ready soybeans in June 2008. In October 2008, soybeans were harvested, and field areas not designated as experimental plots were seeded to a 32-species prairie mix (see Table S1, Supporting information) with forb seeding rates doubled. In May 2009, plots were randomly seeded using a no-till grass drill with one of four vegetation treatments: (i) Switchgrass1 (*Panicum virgatum* monoculture), (ii) Grasses5 (five warm-season grasses), (iii) Biomass16 (16 grass and forb species) or (iv) Prairie32 (32 graminoid and forb species) (see Table S1). Each vegetation treatment was replicated four times on each soil (see Fig. S1). Perennial agroenergy crops are not yet widely produced commercially in the Midwestern USA. The four vegetation treatments described here are trial crops being studied for their yield, feedstock quality and ecosystem service benefits. Hereafter, we refer to Switchgrass1 and Grasses5 collectively as 'grass plots' and to Biomass16 and Prairie32 as 'prairie plots'.

In July 2009, fields were mowed at 10 cm to reduce competition with annual weeds and promote native plant establishment. Buffer strips of cool season vegetation were seeded (11.2 kg ha⁻¹) around each field and in lanes between plots. Lanes were mowed periodically throughout the study. No fertilizers or pesticides were applied in 2009 or 2010.

Our experimental design generated heterogeneity in vegetation structure and composition at two spatial scales. The random assignment of vegetation treatments to plots generated fine-scale compositional heterogeneity within fields. We also predicted that variation in edaphic characteristics among soils would generate structural and compositional heterogeneity among fields (see Fig. S1). Assessing animal response to this soil-induced heterogeneity is the focus of this study. Because we could not randomly assign soil types to plots nor replicate soils within spatial blocks, we are not able to isolate soil from purely spatial effects. Landscape composition and proximity to wooded habitats are known to influence bird and butterfly use of grasslands (Davis, Debinski & Danielson 2007; Renfrew & Ribic 2008); however, our experimental design aimed to minimize variation in such variables that may have influenced use of the plots. For example, there was little variation in landscape composition in 1500-m buffers around the fields (all contained 32–39% cropland, 31–36% forest and 11–13% grassland), and the plot perimeter adjacent to a woody edge (Mean \pm SD: 58.9 \pm 48.4 m) did not vary among soils.

SOIL AND HABITAT SAMPLING

Before seeding in May 2009, three soil cores were collected at three to eight locations within each plot. Cores from each location were combined into one sample, and soil organic carbon (SOC), total nitrogen (TN), pH, bulk density and Mehlich-III extractable macro- (P, K, Ca, Mg and S) and micronutrients (B, Cu, Fe, Mn and Zn) were quantified using appropriate methods (see Appendix S1 for detailed methods).

In 2010, we sampled vegetation structure and composition in a 50 \times 6 m strip transect in each plot (see Appendix S1 for detailed methods). In late May, we measured ground cover (% bare ground, % litter), canopy coverage of plant functional groups (% live grasses, live forbs and standing dead vegetation), litter depth (cm) and visual obstruction readings (VOR, cm). We sampled the species richness of forbs in bloom and the number of inflorescences of each species during five 3-week survey periods from June to September. In September, we sampled above-ground biomass in 10 randomly placed 0.1-m² clip quadrats in each plot. Clippings were sorted by plant functional group, dried at 60 °C for 3 days and weighed.

BIRD AND BUTTERFLY SURVEYS

We conducted repeated, visual surveys of birds and butterflies in 2010 (see Appendix S1 for detailed methods). We surveyed each plot for birds nine times between 1 May and 30 July and for butterflies 10 times between 1 June and 30 September. For birds, we walked (12 m min⁻¹) transects bisecting the plots parallel to their

Table 1. Description of soil series included in the Black Hawk County, Iowa field experiment (NRCS 2015)

Soil series	Parent material	Drainage class	Available water capacity	Taxonomic class
Flagler	Sandy alluvium	Somewhat excessively drained	Low	Fine-loamy over sandy or sandy-skeletal mesic Typic Hapludolls
Waukee	Loamy alluvium	Well-drained	Moderate	Coarse-loamy mesic Phaclic Hapludolls
Spillville–Coland	Loamy alluvium	Somewhat poorly drained	High	Fine-loamy mesic Cumulic Hapludolls/Endoaquolls

longest dimension and recorded the identity, location, and behaviour of all birds observed or heard within the plot. For butterflies, we walked (10 m min^{-1}) $50 \times 6 \text{ m}$ strip transects and recorded the identity, location, and behaviour of all butterflies within a 3-m window around the observer. Butterflies were identified on the wing when possible; otherwise, they were captured and identified in the field or laboratory.

STATISTICAL ANALYSES

Data from soil subsamples were averaged to generate plot means for each measured soil property. We tested for differences in soil property means among soils using one-way analysis of variance (ANOVA). Some variables violated ANOVA assumptions, but all test results were robust to parametric or nonparametric methods, so we report ANOVA results here. For these and all subsequent ANOVAs, we assessed differences among groups using Tukey's HSD pairwise comparisons. Because there was a high degree of collinearity among the 14 soil variables, we conducted canonical analysis of principal coordinates (CAP) to characterize multivariate differences in soil properties among the *a priori* defined soil types and to generate a reduced variable set for subsequent linear regression analyses (Anderson & Willis 2003; Anderson, Gorley & Clarke 2008).

Using quadrats as subsamples, we calculated plot means for bare ground cover (%); litter depth (cm); forb, grass and standing dead cover (%); VOR (cm); VOR coefficient of variation (VOR CV); and total biomass (g cm^{-2}). To quantify floral resource abundance, we summed the average number of inflorescences of each species per m^2 in each plot over the five survey periods. We pooled the data from all five periods, tallied the total number of forb species observed in bloom in each plot, and calculated Shannon's diversity index (H) as a measure of floral diversity. We excluded the grass plots from analyses of floral resources. We conducted two-way ANOVA to assess variation in habitat variables among vegetation treatments and soil types. Litter depth, VOR, total biomass and flower abundance of individual plants were log-transformed prior to analysis. We assessed relationships between soil property CAP scores and selected habitat variables using linear regression.

Using surveys as subsamples, we calculated average total bird and butterfly abundance and the average abundance of each species in each plot. Because plot area was variable, we converted bird counts to densities (birds ha^{-1}); butterfly strip transects were of uniform area, so no conversion was necessary. We pooled data from all surveys to calculate total bird and butterfly species richness and Shannon's diversity index for each plot. We employed two-way ANOVA to test for differences in bird and butterfly abundance, species richness, and diversity by vegetation treatment and soil type. We assessed variation in bird and butterfly assemblage composition using distance-based permutational ANOVA (PERMANOVA). We square-root-transformed the raw abundance data to reduce the influence of dominant species, generated a Bray-Curtis dissimilarity matrix, and conducted multivariate PERMANOVA with 9999 permutations and vegetation treatment and soil type as fixed factors. We performed pairwise comparison tests and generated Monte Carlo P values for significant interactions (Anderson, Gorley & Clarke 2008).

The random assignment of vegetation treatments to plots within soils resulted in the clustering of single treatments within fields (see Fig. S1), possibly influencing bird and butterfly habitat use. To account for this, we summed the total area of adjacent plots of the

same treatment and included this 'patch size' covariate in the ANOVA and PERMANOVA analyses described above. In all cases, patch size explained little variation in our response variables ($P > 0.10$) and its inclusion did not significantly improve model fit, so we report all results from models without the patch size covariate.

We employed non-metric multidimensional scaling (NMDS) to visualize patterns of variation in assemblage composition by vegetation treatment and soil type (Anderson, Gorley & Clarke 2008). To further examine the significant vegetation treatment \times soil type interactions, we generated NMDS plots using subsets of only the grass plots for birds and only the prairie plots for butterflies. To examine relationships between habitat characteristics and bird or butterfly assemblage composition, we added vector overlays depicting Spearman rank correlations of habitat variables to the NMDS axes and generated bubble plots to visualize the contributions of selected species to differences in assemblage structure among the vegetation treatment \times soil type groups. Finally, we employed linear regression to examine relationships between the abundance of selected flowering plants and butterflies. Statistical analyses were performed using R (R Core Team 2013) and PRIMER 6 (version 6.1.13) with PERMANOVA+ (version 1.0.3) (Primer-E Ltd., Plymouth, UK) software.

Results

SOILS AFFECT VEGETATION STRUCTURE AND COMPOSITION

Soil chemical and physical properties varied significantly among the three soil types. Most macro- and micronutrient concentrations were greatest in clay loam, intermediate in loam, and lowest in sandy loam (see Table S2). Exceptions were P and Mn (lower in loam than the other two soils) and K and Cu (similar in all soils). Sandy loam was more acidic with lower bulk density compared to the other soils. Canonical analysis of principal coordinates using the first four ordination axes captured 100% of the original variation in soil properties with a cross-validation allocation success rate of 97.9%. The first CAP axis discriminated soil properties of sandy loam from loam and clay loam; SOC, TN, pH, bulk density, Ca, Mg, S, B and Fe were negatively correlated with CAP1 scores (see Fig. S2). The second CAP axis discriminated loam from clay loam and sandy loam; P and Mn were positively correlated with CAP2.

Soils strongly affected vegetation structure and composition. Generally, plots on loam and clay loam were characterized by taller, more uniformly dense vegetation with abundant residual standing dead vegetation and litter accumulation, whereas plots on sandy loam had more bare ground with shorter, patchier vegetation and sparse litter accumulation (Fig. 1; see Table S3). Mean litter depth was $c. 2\times$ greater and VOR and standing dead cover $c. 3\times$ greater on loam and clay loam than sandy loam. Conversely, bare ground cover and VOR CV were $c. 40\%$ greater on sandy loam than the other soils. Soil property CAP1 scores explained a significant amount of variation in litter depth ($F_{1,45} = 57.2$, $P < 0.001$, $r^2 = 0.54$), VOR ($F_{1,45} = 72.5$, $P < 0.001$, $r^2 = 0.60$), standing dead cover ($F_{1,45} = 14.2$,

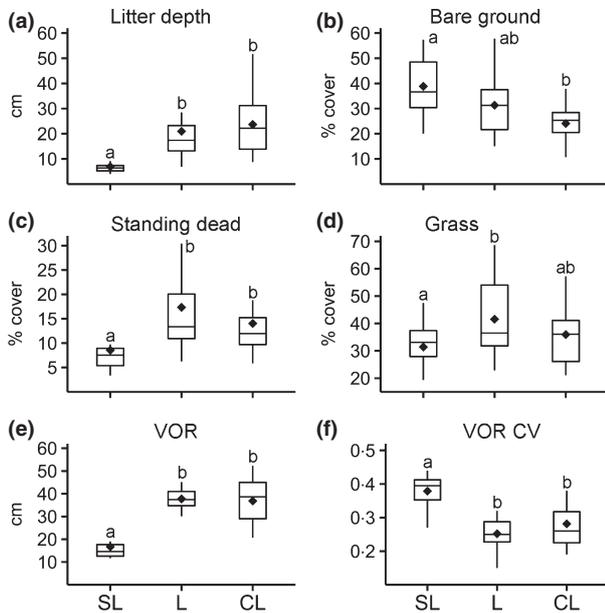


Fig. 1. Boxplots of (a) litter depth, (b) bare ground cover, (c) standing dead cover, (d) grass cover, (e) visual obstruction readings (VOR) and (f) VOR coefficient of variation (VOR CV) by soil type. Box boundaries indicate interquartile range; whiskers indicate 90th and 10th quantiles. Within boxes, horizontal line indicates the median; diamond indicates the mean. Boxes labelled with different letters had means significantly different at $\alpha = 0.05$. SL, sandy loam; L, loam; CL, clay loam.

$P < 0.001$, $r^2 = 0.22$), bare ground cover ($F_{1,45} = 10.6$, $P = 0.002$, $r^2 = 0.17$) and VOR CV ($F_{1,45} = 14.8$, $P < 0.001$, $r^2 = 0.23$).

In prairie plots, flower abundance and species richness were similar among soils, but forb cover and flower diversity were greater on loam and clay loam than on sandy loam (see Table S3). The species composition of forbs in bloom varied among soils (Pseudo- $F_{2,18} = 12.08$, $P < 0.001$), with *Heliopsis helianthoides*, *Ratibida pinnata* and *Oligoneuron rigidum* proportionally more abundant on loam and clay loam and *Desmodium canadense* and *Phlox pilosa* on sandy loam (Fig. 2; see Table S3). Soil property CAP1 scores explained much of the variation in *H. helianthoides* and *D. canadense* abundance (Fig. 3a,b).

BIRDS RESPOND TO HABITAT VARIATION AMONG SOILS IN GRASS PLOTS

We recorded 1036 bird observations representing 22 species (see Table S4). Average bird abundance ($F_{3,36} = 6.66$, $P = 0.001$) and species richness ($F_{3,36} = 7.72$, $P < 0.001$) were greater in prairie plots than in grass plots, and diversity ($F_{3,36} = 5.50$, $P = 0.003$) was greater in Prairie32 than in grass plots. We did not detect a significant effect of soil type on bird abundance, richness or diversity, either as a main effect or interacting with vegetation treatment. However, there were significant differences in bird assemblage composition among soils with a strong vegetation treatment \times soil type interaction, and soils explained more of

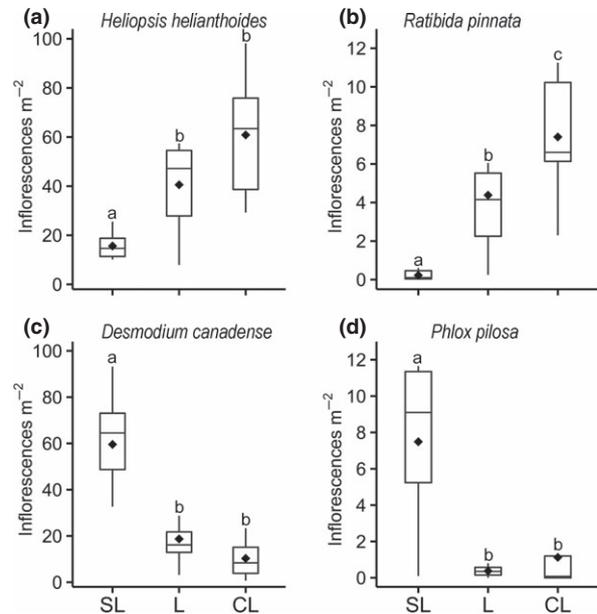


Fig. 2. Boxplots of (a) *Heliopsis helianthoides*, (b) *Ratibida pinnata*, (c) *Desmodium canadense* and (d) *Phlox pilosa* flower abundance in prairie plots by soil type. See Fig. 1 for boxplot interpretation.

the variation in bird assemblage composition than did vegetation treatment (Table 2a). Two main features of the interaction were evident from the NMDS plot and pairwise comparisons (see Fig. S3; Table 3). First, bird assemblage composition varied significantly among the prairie and grass plots on loam and clay loam, while assemblages were similar among all vegetation treatments on sandy loam. Secondly, in grass plots, the bird assemblage using sandy loam was distinct from the assemblages using loam and clay loam (Fig. 4a).

Bird assemblages using sandy loam had greater proportional representation from *Chondestes grammacus* (Fig. 4b), *Spizella passerina* (Fig. 4c), *Zenaida macroura* and *Molothrus ater*, whereas *Cistothorus platensis* (Fig. 4d), *Melospiza melodia* (Fig. 4e), *Spinus tristis*, *Passerina cyanea* and *Geothlypis trichas* were proportionally more abundant on loam and clay loam (see Table S4). Although some habitat characteristics varied between Switchgrass1 and Grasses5 (see Table S3), soil-induced variation in vegetation structure was more influential in structuring bird assemblages using grass plots. In the NMDS plot, all measures of vegetation height and density, including VOR, biomass, litter depth, and standing dead, litter, and grass cover, increased in ordination space moving towards the loam/clay loam plots, whereas bare ground, VOR CV and forb cover increased in the direction of the sandy loam plots (Fig. 4a).

BUTTERFLIES RESPOND TO HABITAT VARIATION AMONG SOILS IN PRAIRIE PLOTS

We recorded 2110 butterfly observations representing 31 species (see Table S5). Average butterfly abundance

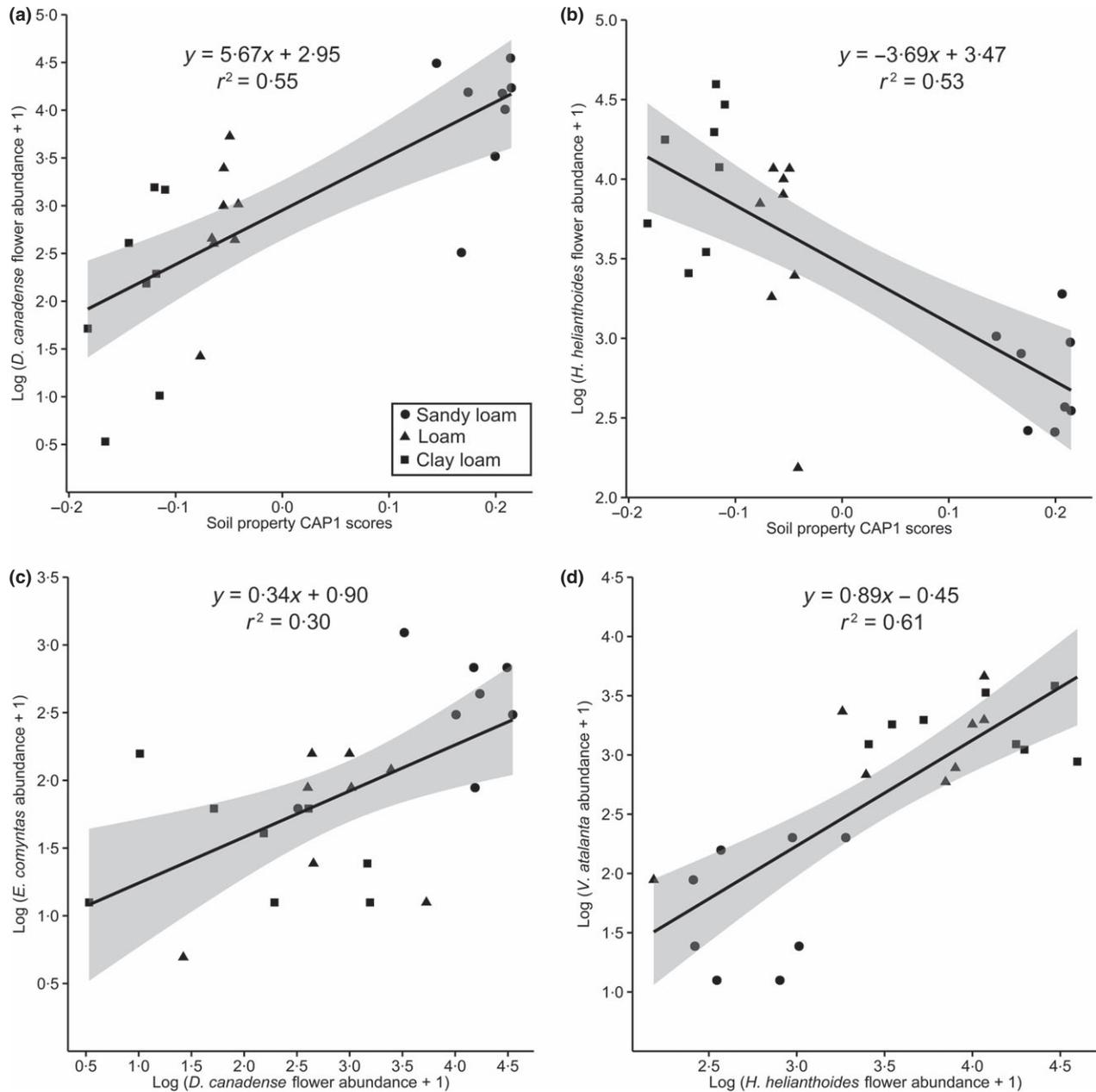


Fig. 3. Relationships between soil property canonical analysis of principal coordinates axis 1 scores (CAP1) and (a) *Desmodium canadense* and (b) *Heliopsis helianthoides* flower abundance, (c) *D. canadense* flower abundance and *Everes comyntas* abundance, and (d) *H. helianthoides* flower abundance and *Vanessa atalanta* abundance in 24 prairie plots on three soil types.

($F_{3,36} = 108.5$, $P < 0.001$) and species richness ($F_{3,36} = 49.9$, $P < 0.001$) were significantly greater in prairie plots than in grass plots but did not vary among soils. Butterfly diversity was greater in prairie plots than in Grasses5 ($F_{3,36} = 4.9$, $P = 0.006$) and on clay loam than on sandy loam ($F_{2,36} = 3.4$, $P = 0.046$). Multivariate analysis of butterfly assemblage composition revealed significant effects of vegetation treatment and soil type with a significant interaction (Table 2b). Vegetation treatment effects were large and consistent across soils (Table 3; see Fig. S4). Butterfly assemblages using prairie plots were distinct from those using grass plots; however, there were no differences

between Biomass16 and Prairie32, nor between Switch-grass1 and Grasses5, on any soil type. Compared to vegetation treatment, soils explained less of the variation in butterfly assemblage composition; however, butterfly assemblages using prairie plots on sandy loam were clearly distinct from those using loam and clay loam, which were similar to one another (Table 3; Fig. 5a). This pattern was not evident in the grass plots, where butterfly assemblages were similar on all soils.

In prairie plots, the butterfly assemblage using sandy loam had greater proportional representation from *Everes comyntas* (Fig. 5b), *Phyciodes tharos* (Fig. 5c), *Colias*

Table 2. PERMANOVA table comparing (a) bird and (b) butterfly assemblage dissimilarity among the four vegetation treatments and three soil types

Source of variation	d.f.	MS	Pseudo- <i>F</i>	<i>P</i>	ECV*
(a) Bird assemblage dissimilarity					
Vegetation treatment	3	3357.7	2.82	0.0001	14.8
Soil type	2	11 915	10.00	0.0001	28.5
Vegetation treatment × soil type	6	2343.3	1.97	0.0011	18.7
Residual	36	1191.2			38.0
(b) Butterfly assemblage dissimilarity					
Vegetation treatment	3	11 683	16.75	0.0001	38.6
Soil type	2	2491.6	3.57	0.0001	13.5
Vegetation treatment × soil type	6	1197.5	1.72	0.0031	14.3
Residual	36	697.4			33.6

*Percentage estimated components of variation.

eurytheme/philodice and *Strymon melinus*, whereas *Vanessa atalanta* (Fig. 5d), *Junonia coenia* (Fig. 5e), *Danaus plexippus* and *Hylephila phyleus* were proportionally more abundant on loam and clay loam (see Table S5). Several measures of vegetation height and density (VOR, litter depth and standing dead and forb cover) and the abundance of *H. helianthoides*, *R. pinnata* and *O. rigidum* flowers increased in ordination space moving towards the loam/clay loam plots, whereas VOR CV and *D. canadense* flower abundance increased moving towards the sandy loam plots (Fig. 5a). The abundance of certain butterflies was clearly related to specific plants whose abundance varied among soils. For example, there were strong linear relationships between soil property CAPI scores and the abundance of *D. canadense* (Fig. 3a) and

H. helianthoides (Fig. 3b) flowers and between the abundance of these flowers and *E. comyntas* (Fig. 3c) and *V. atalanta* (Fig. 3d), respectively.

Discussion

Birds and butterflies responded to habitat heterogeneity generated by our experiment at two spatial scales: (i) fine-scale heterogeneity within fields generated by our experimental vegetation treatments, and (ii) larger-scale heterogeneity among fields generated by differences in soil properties. The documentation of indirect, vegetation-mediated effects of soil properties on the spatial distribution of higher trophic levels is the most novel result of our research. We found that variation in edaphic characteristics generated habitat heterogeneity during perennial grassland establishment, even in the absence of disturbances known to promote heterogeneity, and that birds and butterflies responded similarly to soil-induced heterogeneity during the transition from annual to perennial crops. Despite differences in average plot size among soils, bird and butterfly abundance and species richness were similar on all soil types; however, their assemblage composition differed among soils, with the effects most pronounced in grass plots for birds and in prairie plots for butterflies.

Vegetation structural characteristics known to influence bird habitat use (Fisher & Davis 2010) varied widely among grass plots on different soils, and birds responded predictably to these differences based on well-documented habitat associations (Johnson, Igl & Dechant Shaffer 2004). Birds found in greater abundance on sandy loam were primarily ground-foraging and nesting species (*C. grammacus*, *S. passerina*, *Z. macroura* and *M. ater*) preferring early successional habitats with abundant bare ground and sparse litter. In contrast, birds more abundant

Table 3. Pairwise comparisons of bird and butterfly assemblage dissimilarity (a) within each vegetation treatment among soils and (b) within each soil type among vegetation treatments

(a)	Switchgrass1 (S1)		Grasses5 (G5)		Biomass16 (B16)		Prairie32 (P32)	
	<i>t</i> _{birds}	<i>t</i> _{butterflies}						
SL-L	2.25*	0.84	2.53**	1.21	1.41	2.76**	1.87*	1.98*
SL-CL	2.15*	1.07	2.55**	1.79	1.66	3.66**	2.07*	2.96**
L-CL	0.61	0.92	1.88*	1.12	1.93*	0.87	1.01	0.99
(b)	Sandy loam (SL)		Loam (L)		Clay loam (CL)			
	<i>t</i> _{birds}	<i>t</i> _{butterflies}						
S1-G5	0.82	1.30	1.21	0.97	0.76	0.96		
S1-B16	1.15	3.64**	2.6**	2.64**	2.19*	2.58**		
S1-P32	1.19	3.35**	2.09*	2.41**	1.88*	2.59**		
G5-B16	1.08	3.17**	1.91*	3.61**	1.96*	3.96***		
G5-P32	1.08	2.85**	2.15*	3.24**	1.83*	4.08***		
B16-P32	0.87	1.65	1.79*	0.62	1.20	1.09		

P* < 0.05, *P* < 0.01, ****P* < 0.001.

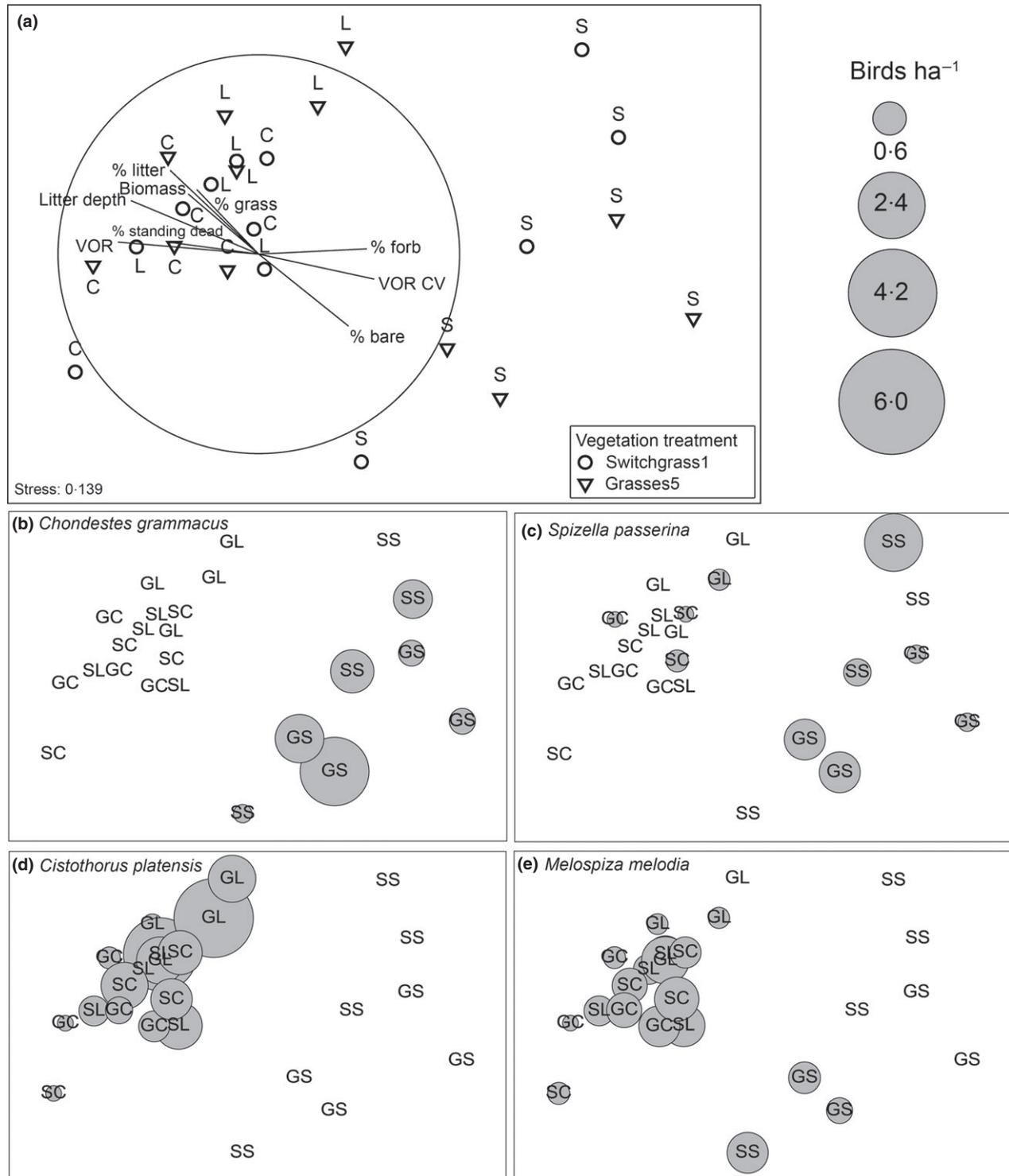


Fig. 4. Non-metric multidimensional scaling (NMSD) of bird assemblage composition in 24 grass plots on three soil types. Vector overlays (a) depict Spearman rank correlations of habitat variables with NMSD axes relative to a unit circle. Bubble plots illustrate differences in (b) *Chondestes grammacus*, (c) *Spizella passerina*, (d) *Cistothorus platensis* and (e) *Melospiza melodia* abundance by soil type. First letter of plot label refers to vegetation treatment: S: Switchgrass1; G: Grasses5; B: Biomass16; and P: Prairie32; and second to soil type: S: sandy loam; L: loam; and C: clay loam.

on loam and clay loam (*C. platensis*, *M. melodia*, *S. tristis*, *P. cyanea* and *G. trichas*) place their nests above ground in live or residual standing dead vegetation, feed by gleaning foliage in addition to ground foraging, and

are generally associated with tall, dense plant communities with abundant litter and standing dead vegetation.

Soil properties influenced plant community composition and vegetation structure in prairie plots, and butterfly

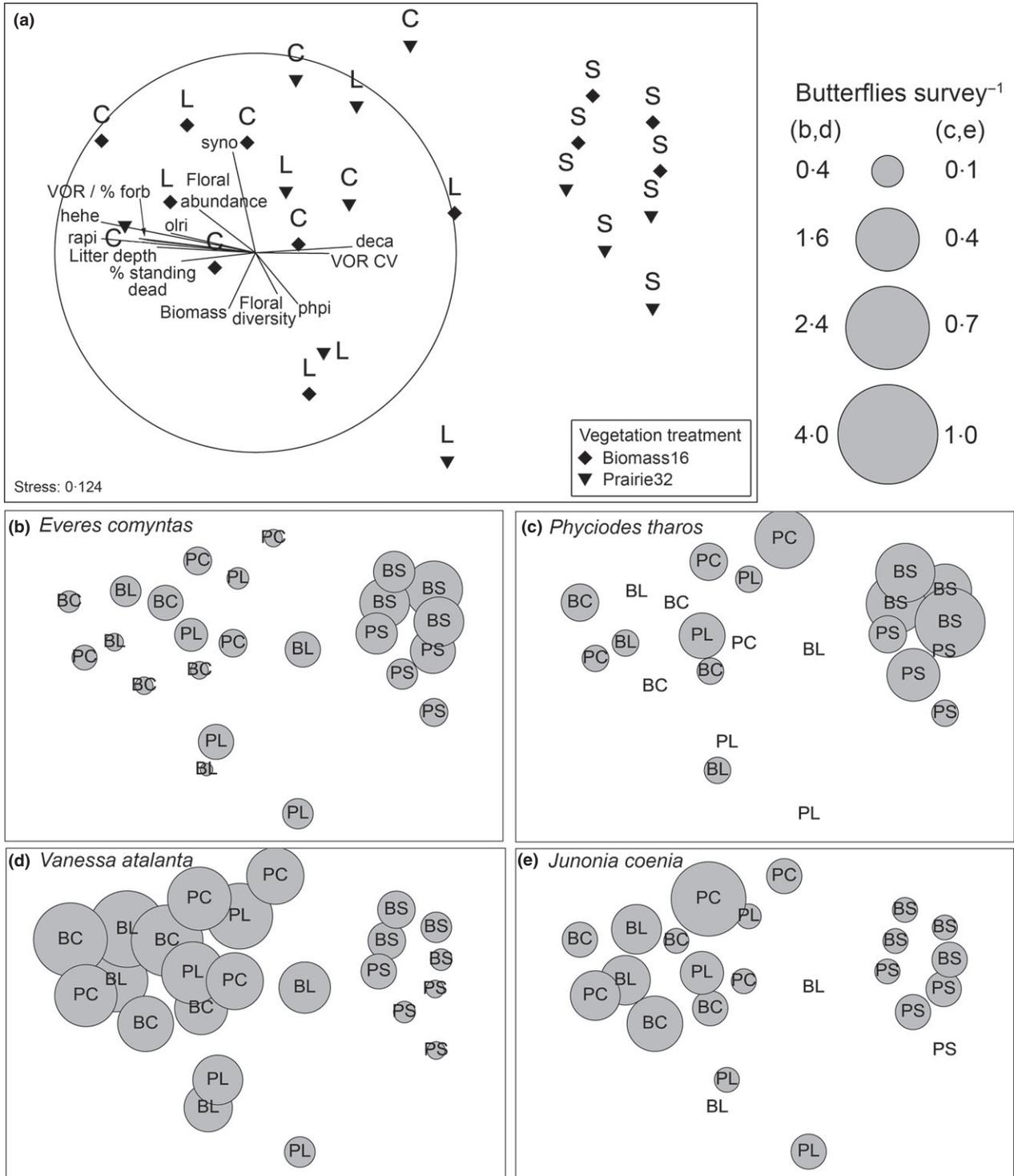


Fig. 5. Non-metric multidimensional scaling (NMSD) of butterfly assemblage composition in 24 prairie plots on three soil types. Vector overlays (a) depict Spearman rank correlations of habitat variables with the NMSD axes relative to a unit circle. Bubble plots illustrate differences in (b) *Everes comyntas*, (c) *Phyciodes tharos*, (d) *Vanessa atalanta* and (e) *Junonia coenia* abundance by soil type. Four-letter codes indicate floral abundance of *Desmodium canadense* (deca), *Heliopsis helianthoides* (hehe), *Oligoneuron rigidum* (olri), *Phlox pilosa* (phpi), *Ratibida pinnata* (rapi) and *Symphytotrichum novae-angliae* (syno). See Fig. 4 for plot labels.

assemblages varied among soil types in response to this heterogeneity. Spatial heterogeneity in plant community composition may be expected to drive differences in butterfly assemblages if plants that vary in abundance are lar-

val hosts or nectar sources for adult butterflies. Our study provides examples of both. For example, *D. canadense*, an *E. comyntas* host plant, was *c.* 4× more abundant on sandy loam than the other soils. Accordingly, the

proportional representation of *E. comyntas* was greater on sandy loam (rank abundance = 2, relative abundance = 17.4%) than on loam (4, 7.5%) or clay loam (6, 4.5%). Likewise, *H. helianthoides* flowers, an important nectar source for butterflies in tallgrass prairie remnants (Bray 1994), were *c.* 3× more abundant on loam and clay loam than on sandy loam, and several of the most common butterflies (*V. atalanta*, *J. coenia* and *D. plexippus*) on these soils were frequently observed feeding on this species. For example, *V. atalanta* was dominant on loam (rank abundance = 2, relative abundance = 27.4%) and clay loam (2, 28.6%), but its frequency of occurrence and relative abundance were much lower on sandy loam (4, 6.9%). Butterfly assemblages also varied in response to heterogeneity in vegetation structure among soils. Past studies have shown *P. tharos*, *E. comyntas* and *S. melinus* abundance to be positively associated with bare ground and negatively associated with litter cover and depth, with the opposite reported for *D. plexippus* (Davis, Debinski & Danielson 2007; Vogel *et al.* 2007). We observed variation in the abundance of these species among soils consistent with these habitat associations.

While our results demonstrate that vegetation structure and composition varied among soils at the community level, previous studies have shown that fine-scale heterogeneity in soil characteristics influences individual plant traits, including above-ground biomass production, photosynthetic efficiency and competitive ability (Baer *et al.* 2003, 2005; Hutchings, John & Wijesinghe 2003; Roiloa & Retuerto 2006). The degree to which soil characteristics affect the quality of individual plants from a butterfly habitat perspective (e.g. nutrient composition or nectar production) is a subject for future research.

IMPLICATIONS FOR MANAGEMENT AND BIODIVERSITY CONSERVATION

Our findings have applied implications for the maintenance of biodiversity in managed prairie agroenergy crops and for the restoration of grassland habitat for wildlife species of conservation concern. Federal mandates for increased agroenergy production are projected to further intensify corn production and dramatically alter land use in the Midwestern USA (Mehaffey, Smith & Van Remortel 2012). While current US agrofuel production is dominated by corn grain ethanol, the establishment of second-generation, perennial crops on non-prime agricultural land has been advanced as an alternative strategy to help meet cellulosic agrofuel targets while promoting soil, water and wildlife habitat conservation (Werling *et al.* 2014). At our experimental site, we found that sitewide bird and butterfly diversity were greater because of the habitat variation among soils than they would have been where the site comprised of a single soil type. Farms in North America's tallgrass prairie region typically have variable topography and wide-ranging soil quality, both

of which are known to influence vegetation structure and biomass yields (Zilverberg *et al.* 2014). Our results suggest that if unfertilized tallgrass prairie crops were grown for agroenergy at the farm scale, variation in topo-edaphic characteristics within and among fields would likely generate heterogeneity detectable by wildlife during establishment, even if a single crop type were planted over a large area. Further, our findings suggest that the practice of characterizing local bird assemblages using perennial crops at the field scale using single, randomly located point counts or strip transects may underestimate avian richness in large fields with wide-ranging soil quality. While our results are restricted to the establishment phase of crop management, the land area of recently established perennial crops could constitute a significant amount of grassland habitat were such production systems ever adopted at large scales. This source of fine-scale heterogeneity has been overlooked in reviews of candidate agroenergy crops (Fargione *et al.* 2009; Fletcher *et al.* 2011) and would further increase the relative habitat value of perennial crops compared to fertilized, annual monocultures that currently dominate the agricultural landscape.

Future research is needed to determine whether the habitat heterogeneity observed among soils is transient during the establishment phase of crop management or whether it will persist long term. We found significant variation in biomass production and litter accumulation among soils. Differential litter production could induce spatial variability in self-disturbance, an intrinsic mechanism known to promote fine-scale heterogeneity in tallgrass prairies (Bascompte & Rodriguez 2000), and increase heterogeneity among soils over time. Conversely, increasing dominance of competitively superior plants (Baer *et al.* 2005) or the application of crop management practices (e.g. prescribed fire, fertilization, harvest) could result in the convergence of habitat characteristics among soils over time. Fertilization of perennial prairie crops may promote uniformly high yields and influence plant diversity (Jarchow & Liebman 2013); however, this management practice would likely homogenize vegetation structure and reduce the habitat value of these crops for wildlife (Wilson, Whittingham & Bradbury 2005), diminish the provisioning of other ecosystem services (Werling *et al.* 2014), and negate some economic benefits derived from the low-input nature of these crops.

The adoption of perennial, cellulosic agroenergy cropping systems on marginal lands has the potential to greatly increase the amount of restored grassland in the Midwestern landscape (Werling *et al.* 2014). Our findings suggest that when particular animal species are being targeted for conservation, identifying soils that will support the establishment and growth of plants in a manner yielding the particular habitat characteristics required by the target species should be considered in selecting candidate sites for grassland restoration. While soil-mediated effects on grassland bird and butterfly habitats have been

recognized in the literature (Askins *et al.* 2007; Titeux *et al.* 2009), we believe that the influence of soils in determining habitat features has been underappreciated in the literature, and we are unaware of past experimental research documenting faunal responses to soil-induced habitat heterogeneity. Our study provides an example of the value of Heneghan *et al.*'s (2008) concept of incorporating 'soil ecological knowledge' in restoration planning. For example, *C. platensis*, an obligate grassland species of greatest conservation need in Iowa, nested successfully and was among the most abundant species using loam and clay loam plots, but we never observed a single individual on sandy loam, presumably because the vegetation height–density was insufficient for this species to recognize those plots as suitable habitat (Johnson, Igl & Dechant Shaffer 2004). Conversely, *C. grammacus* was a dominant species in grass plots on sandy loam but was completely absent on loam and clay loam because the tall, dense canopy and abundant litter accumulation on these soils were negative habitat cues for this early successional species (Johnson, Igl & Dechant Shaffer 2004). If we aimed to restore habitat for either species, our results suggest that selecting sites with appropriate soils would determine the immediate success or failure of habitat management efforts.

Bird abundance and species richness in candidate Midwestern perennial agroenergy crops have been positively associated with increased forb cover and vegetation structural diversity at the field scale (Robertson *et al.* 2011; Blank *et al.* 2014). Our experimental design created a mosaic of vegetation treatments with artificially high compositional and configurational heterogeneity (Fahrig *et al.* 2011) within fields compared to real-world systems where entire, larger fields would likely be planted to single crops. We found, however, that bird and butterfly abundance and species richness varied greatly among vegetation treatments, suggesting that individuals were responding to patch-level variation in habitat characteristics within fields by disproportionately selecting certain vegetation treatments for foraging and/or reproduction. This finding suggests that fine-scale heterogeneity in vegetation structure and composition within fields, whether due to natural topo-edaphic variation or resulting from management activities (e.g. rotational harvest), will strongly influence ecological interactions in perennial agroenergy crops (Benton, Vickery & Wilson 2003; Pickett & Siriwardena 2011).

Finally, we frequently observed bird nesting activity and butterfly oviposition in the plots, but we were not able to assess reproductive success or source–sink dynamics at the population level. Future studies of bird and butterfly reproductive ecology at the broad spatial scales at which i) perennial agroenergy crops are sown commercially in practice and ii) bird and butterfly assemblages are genuinely supported for breeding are needed to assess the true habitat quality of perennial agroenergy crops relative to other grasslands in the region.

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Data accessibility

Data analysed in this manuscript are archived at Dryad Digital Repository, doi: 10.5061/dryad.4ft7n (Myers *et al.* 2015).

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Supporting Information

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

Appendix S1. Supplementary text for Materials and Methods.

Figure S1. Map of study site.

Figure S2. Soil property CAP ordination.

Figure S3. Bird assemblage NMDS ordination.

Figure S4. Butterfly assemblage NMDS ordination.

Table S1. Vegetation treatment seed mixes and seeding rates.

Table S2. Soil properties.

Table S3. Habitat characteristics by vegetation treatment and soil type.

Table S4. Bird assemblage composition by vegetation treatment and soil type.

Table S5. Butterfly assemblage composition by vegetation treatment and soil type.