Land-use history and an invasive grass affect tallgrass prairie sedge community composition

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Abstract

Questions: How abundant and diverse are sedges in upland tallgrass prairie? Are sedge communities associated with historical land use, abundance of an invasive species or different fire and grazing management regimes? How do sedge communities compare between reconstructed and intact grassland?

Location: Grand River Grasslands; working tallgrass prairie in north-central Missouri and south-central Iowa (US).

Methods: From 2008 to 2010, we surveyed the sedge species richness and measured canopy cover (an estimate of abundance) on 13 tallgrass prairie tracts, and measured canopy cover of an invasive C_3 grass, tall fescue (*Schedonorus phoenix* (Scop.) Holub). Flowering sedges were identified to species and associated with wetland indicator status (WIS) and coefficients of conservatism (CoC). We calculated mean WIS, CoC, species richness (observed and estimated) and diversity (1/Simpson's D) for each tract. We used linear mixed-effect regression and multivariate ordination to describe patterns of sedge abundance and community composition in terms of land-use history (previously severely grazed intact prairie; previously ungrazed intact prairie; and reconstructed prairie), tall fescue abundance and current management (patch burn-grazed, burned-and-grazed burned only).

Results: On average, sedges constituted $20 \pm 0.01\%$ of total plant abundance. Sedge abundance increased over time and was higher on intact prairie than on reconstructions, but grazing history of intact prairie did not affect sedge abundance. We observed 21 species that averaged moderate wetland affinity (mean WIS = -2.1 ± 0.2) and moderate affinity for undisturbed habitat (mean CoC = 4.5 ± 0.2 and 5.0 ± 0.1) from Iowa and Missouri lists, respectively). Species richness, diversity and conservatism did not vary with land-use history, current experimental management or tall fescue abundance, although all three variables were associated with patterns of sedge community composition.

Conclusions: Diverse and abundant sedge communities provide a substantial forage resource for early season grazing. Neither historical grazing nor current fire/grazing management affected sedge diversity or floristic integrity. These data suggest grazing and the degree of invasion do not necessarily degrade entire native plant communities – responses likely vary among plant groups – but land-use legacies have a persistent effect on sedge community composition.

Introduction

The botanical family Cyperaceae – grass-like flowering plants known as sedges – includes over 5000 species in ca.100 genera, and ranks among the world's most ubiquitous and diverse taxonomic groups (Goetghebeur 1998).

However, little research has explored the community and disturbance ecology of sedges. When sedges are included in such studies, they are often considered a single functional group (e.g. Coppedge et al. 1998a; Shay et al. 2001). The tendency to overlook sedge species identities and consider sedges as a group is understandable, given

the difficulties in discerning sedge species, but there is little evidence that species-specific ecology is sufficiently homogeneous to justify an otherwise arbitrary sedge morpho-category.

Sedges are often associated with low-lying, undisturbed natural habitats (Grime 1984; Fitter 2005). Consistent with conventional wisdom, most sedge ecology field studies come from wetlands, peatlands and wet meadows (Gignac et al. 2004; Ssegawa et al. 2004; Allessio Leck & Schütz 2005; Kettenring 2006), or specifically consider soil moisture gradients (Vellend et al. 2000). As such, these studies primarily discuss soil moisture, nutrient availability, dispersal and niche differentiation as drivers of sedge diversity.

Several studies highlight the forage value of sedges, but relatively few address the impact of management on sedge abundance and community composition. In North America, sedges are an important forage resource for bison (Coppedge et al. 1998b; Harvey & Fortin 2013), and certain sedge species are recognized as important livestock forage in western rangeland (Holechek et al. 1982; Clark 2003). Studies testing sedge response to prescribed fire in northern mixed-grass prairie report variable species-specific responses to different fire intervals and seasons (Gross & Romo 2009) and a neutral or reducing effect of fire on sedge abundance (Anderson & Bailey 1980; White & Currie 1983).

In this study we report sedge abundance, species diversity and community composition in central North American tallgrass prairie, with respect to fire and grazing management and abundance of an invasive C_3 grass. With little previous work on sedge community ecology to inform our predictions, we draw from a broad literature that documents the effects of fire, grazing and invasive species on herbaceous vegetation. Work from the region describes fire as a disturbance that reduces plant diversity while grazing increases diversity (Collins 1987; Collins et al. 1998), although the specific effects of fire and grazing vary with intensity, frequency and spatial pattern of each disturbance (Collins 1992, 2000; Hickman et al. 2004; Collins & Smith 2006; Bowles & Jones 2013). While several introduced forage species are invasive in the study area, tall fescue [Schedonorus phoenix (Scop.) Holub] is especially abundant and has been associated with reduced native plant species richness (Rudgers et al. 2005; McGranahan et al. 2012, 2013).

We also compare sedge abundance and community composition across tracts with different land-use histories, specifically those with and without severe livestock grazing, and post-agriculture prairie reconstructions. In our study area, historically severe grazing, specifically, affects plant community composition (McGranahan et al. 2013) and modulates ecosystem response to management (Debinski et al. 2011; Moranz et al. 2012). Land-use legacies can persist for decades and alter ecosystem functioning

and vegetation patterns (Bellemare et al. 2002; Fraterrigo et al. 2005). These persistent effects confound management by altering restoration trajectories and complicate research by introducing variation among treatments, but land-use legacies must be understood and used to explain current ecological conditions and inform effective restoration action (Foster et al. 2003; Cramer et al. 2008).

Row-crop agriculture has also degraded much of the tallgrass prairie, with such a persistent legacy that native plant communities must be deliberately reconstructed. Sedges, however, are rarely included in restoration efforts (Houseal & Smith 2010). Although studies have described differences in diversity and composition of sedge communities across natural and restored wetlands (Galatowitsch & van der Valk 1996; Kettenring & Galatowitsch 2011; Van der Valk 2013), sedge communities of reconstructed upland grassland remain undescribed in the region.

We use sedge species richness, Simpson's diversity index and multivariate methods to test the following predictions: (i) historically severe grazing reduces sedge abundance and diversity and alters community composition; (ii) reconstructed prairie has lower sedge abundance, lower diversity and different community composition than intact grassland; and (iii) under current management, recent fire reduces sedge abundance.

Methods

Study area

Data come from the Grand River Grasslands of Ringgold County, Iowa, and Harrison County, Missouri (40.572650° N, 94.171466° W), a working landscape in which grazing and row-crop agriculture occur alongside conservation management areas (Miller et al. 2012). Soils belong to the Gara-Armstrong-Pershing association, and study tracts were dominated by two upland soil types, Gara loam and Armstrong loam (USDA-NRCS 2010). Annual precipitation averages ca. 910 cm (IEM 2011). Native plant species – principal grasses: Sorghastrum nutans (L.) Nash, Andropogon gerardii Vitman, Sporobolus clandestinus (Biehler) Hitchc. and Schizachyrium scoparium (Michx.) Nash; principal forbs: Solidago canadensis L. and Vernonia baldwinii Torr. – comprise ca. 70% of non-sedge plant species richness in study tracts, while several exotic forages – grasses: Schedonorus phoenix (Scop.) Holub, Poa pratensis L. and Bromus inermis Leyss.; forbs: Medicago lupulina L. and Kummerowia striata (Thunb.) Schindl. – comprise the remainder (McGranahan et al. 2013).

Experimental design

The study comprised 13 grassland tracts (15–31 ha) representing a spectrum of historical and current management.

All tracts have been managed as experimental grasslands in a fire and grazing study initiated in 2006 (e.g. Moranz et al. 2012), and thus historical and current management refers to use prior to 2006 and experimentally managed disturbance regime since 2006, respectively.

We divided historical land use into three classes based on interviews with current and previous landowners and managers (McGranahan et al. 2012, 2013): intact prairie, previously grazed up to 15 animal unit months ha^{-1} within at least 5 yr before study initiation (2000–2006) (five tracts); intact prairie previously ungrazed 2000–2006 (five tracts); and reconstructed prairie (three tracts; Table 1). Both classes of intact prairie refer to grassland not known to have been subject to severe biophysical disturbance to the soil–vegetation matrix, such as cultivation. The native plant community of reconstructed prairie derives from post-agricultural re-vegetation. Fire histories prior to 2006 were not quantified, but previously ungrazed tracts have long been burned on a 2–3 yr fire return interval, consistent with grassland management in the area.

Each tract was assigned to one of three experimental disturbance regimes (Table 1): *patch burn-grazed*, in which one third of the tract was burned annually, with cattle (*Bos taurus*) grazing managed at moderate stocking rates; *burned-and-grazed*, in which the entire tract was burned every third year and moderately stocked with cattle; and *burn only*, in which the entire tract was burned every third year but not stocked with cattle. Moderate cattle grazing, which spanned May through September annually, began

in 2006, while patch-burn fire treatments began in spring 2007. Entirely burned pastures – both grazed and ungrazed – were burned in spring 2009.

Treatment design followed an unbalanced factorial design with four pastures per treatment. Patches constituted the experimental unit. Infrastructure limitations (fence, water access) and management agreements restricted which pastures could be grazed, but within those available for grazing patch burn-grazing and burned-and-grazed were randomly assigned. These same limitations also limited our ability to fully cross grazing treatments with grazing history; thus historically grazed pastures all continued to be grazed, while some historically ungrazed pastures (Lee Trail, Ringgold South) were experimentally grazed.

Data collection

Vegetation surveys were conducted late May–early June during 3 yr from 2008 to 2010. Within each tract, we sampled six permanently placed, 25 m × 20 m modified Whittaker plots (Stohlgren et al. 1998). All tracts were partitioned into three equal-sized patches, with two modified Whittaker plots per patch (McGranahan et al. 2012, 2013; Moranz et al. 2012). Aside from contrasts between burned and unburned areas in patch burn-grazed tracts, patch boundaries were not physically demarcated. Within patches, one plot was located on each of the two dominant soil types, with most plots situated halfway up slopes or on

Table 1. Land-use history and current treatment for 13 tallgrass prairie tracts, and summarized diversity statistics for Cyperaceae communities. Previous grazing history refers to 5 yr prior to study initiation (2000–2006).

Land-use History	Tract	Current treatment	1/Simpson's D	Wetland indicator status	Coefficient of conservatism		Species richness		
					Iowa	Missouri	Mean	Total	Estimated
Intact, Previously grazed			3.0 (±0.5)	−2 (±0.2)	3.9 (±0.1)	5.1 (±0.2)	8.8 (±1.1)	14	16 (±2)
	Gilleland	Burned-and-grazed	4.0	−2.9	4.1	5.0		7	
	Jerome	Patch burn-grazed	4.3	−1.5	3.8	4.6		13	
	Pyland North	Patch burn-grazed	1.8	−1.2	4.0	4.9		9	
	Pyland South	Patch burn-grazed	2.7	−1.6	3.9	5.1		7	
	Pyland West	Burned-and-grazed	2.2	−2.7	3.6	5.6		8	
Intact, Previously ungrazed			3.6 (±0.5)	−2.1 (±0.4)		4.5 (±0.2)	9.8 (±1.0)	19	25 (±3)
	Lee Trail	Burned-and-grazed	5.1	−1.6	3.9	5.2		13	
	Pawnee	Burn only	3.5	−2.9	3.5	4.6		10	
	Richardson	Burn only	2.7	−2.7	4.3	4.4		9	
	Ringgold North	Burn only	2.5	−2.3	3.4	3.7		7	
	Ringgold South	Patch burn-grazed	4.4	−1.0	3.3	4.6		10	
Reconstructed prairie			2.3 (±0.6)	−2.5 (±0.2)	4.6 (±0.3)	4.6 (±0.1)	7.0 (±3.0)	12	17 (±6)
	Kellerton	Patch burn-grazed	1.4	−1.8	4.8	4.5		4	
	Sterner	Burned-and-grazed	3.4	−3.1	4.2	4.8		13	
	Tauke	Burn only	2.1	−2.5	5.0	4.5		4	

the shoulder of slopes, and no plots were located at the bottom of slopes or on hilltops.

Each modified Whittaker plot contained ten, 0.5-m² subplots, within which we visually estimated abundance of each plant species with Daubenmire's (1959) canopy cover method. Although data on all plant species were collected, this paper considers only presence and abundance of Cyperaceae (sedges) and tall fescue abundance. For sedges, specifically, two classes of data were collected: first, we recorded the combined abundance of all sedges present, with and without flowers; second, we collected specimens (whole tillers including subsoil organs when possible) of each different sedge species in flower, assigned each a unique code and recorded the canopy cover of each coded flowering sedge. We also recorded the presence of additional sedge species beyond the ten 0.5-m² subplots but within the 500 m² plot boundary; these species were assigned a canopy cover value of 0.1, while canopy cover values for each species within the ten 0.5-m² subplots were averaged.

Specimens from the field were mounted, and after the third and final field season, a two-part process was initiated to identify sedge specimens to species. First, J.T. Mulloy used leaf, flower and seed morphology to identify one to three potential species per sample for as many field samples as possible. Second, these preliminary identifications were evaluated by T.R. Rosburg, Drake University, Des Moines, IA, US, an expert on sedges in the study region, who returned genus and species designations following the Flora of North America North of Mexico (1993). As patches were the experimental unit in the study, we calculated the maximum abundance for each sedge species and the average tall fescue abundance from both plots within each patch, and combined across all 3 yr.

To help understand the ecology of the species we identified, we combined data from publically available databases on wetland indicator status and dependence on undisturbed habitat. Wetland indicator status ranges from wetland obligates, which almost always occur in wetlands, to upland obligates, which almost never occur in wetlands, according to the National Wetland Plant List (Lichvar 2013). We also report coefficients of conservatism (CoC), which indicate a species' tolerance for human-mediated disturbance on a scale from 0 (high disturbance tolerance, low habitat specificity) to 10 (low disturbance tolerance, strong affinity for natural plant communities; Swink & Wilhelm 1994). Mean CoC is an indicator of overall floristic integrity for a sampled unit (Taft et al. 2006). Because CoC is determined for species at the state level, and the Grand River Grasslands occur in both Iowa and Missouri, we used both Iowa and Missouri CoC as presented by the Iowa State University Herbarium (http://www.public.iastate.edu/~herbarium/Cofcons.xls).

Data analysis

Overall abundance

To determine which factors affected sedge abundance, we tested combined sedge canopy cover for each modified Whittaker plot against historical and current management variables using a multiple linear mixed-effect (LME) regression model. Independent variables included tall fescue canopy cover, previous grazing history, current treatment, time-since-fire (since 2007) and sample year. Continuous variables (sedge and tall fescue canopy cover) were scaled to facilitate comparison of beta regression coefficients, the absolute values of which were used to determine the relative importance of variables to explaining variation within the model (Enders & Tofighi 2007). To create the LME model, we used the lme function in the nlme package for the R statistical environment (R Foundation for Statistical Computing, Vienna, AT). In all statistical tests, no comparisons or trends are considered different when $P \geq 0.05$. In discussion of tests where $P < 0.05$, the terms vary and difference are used synonymously with 'statistically significant difference'.

To identify terms most relevant to variation in sedge abundance, we used the R step-wise model selection function stepAIC. stepAIC begins with the full LME model (all independent variables listed above) and sequentially removes and re-combines variables to select a set that minimizes the Akaike information criterion (AIC) of the final model. Difference between the full and selected models was tested with the ANOVA function. To compare variation explained by the full and selected LME models, we used a custom function, r.squared.lme (App. S1) to calculate determination coefficients (R^2) following Nakagawa & Schielzeth (2013). The function calculates marginal R^2 values from variance components from the LME model that represent the goodness-of-fit for the combination of independent variables.

Because most of the independent variables (all except tall fescue canopy cover) were categorical factors, we compared each with post-hoc Tukey tests based on each LME model using the glht function in the multcomp library for R. Complete R code is available in App. S1.

Species richness, diversity and conservatism

To describe sedge diversity, we applied a suite of diversity analyses to the combined data set of all identified sedge samples from all years. We calculated the following basic descriptive statistics for each tract: species richness (S), species proportional abundance (p_i), the inverse Simpson's diversity index ($1/D$; $D = \sum p_i^2$) and mean CoC.

To compare species richness and diversity statistics across grazing history groups (previously grazed, previously ungrazed, reconstruction) and current treatment groups (patch burn-grazed, burn-and-grazed, burn only), we first created LME regression models with each measure as response variables, history and treatment as predictor variables, and tract as a random effect. Second, we compared groups with *post-hoc* Tukey tests using the glht function. We also used this procedure to test each variable against tall fescue abundance.

Because not all samples were identified – and not all species were flowering during sampling – we estimated the number of undetected species for each land-use history group. We used the specpool function in vegan, which estimates total species richness (observed + undetected) through extrapolations based on the number of rare species in the observed species pool. We report the first-order jackknife estimate based on its low bias and high precision (Palmer 1990).

Multivariate community composition

To analyse sedge community composition, we used an unconstrained ordination, non-metric multi-dimensional scaling (NMDS), performed with the vegan function meta-MDS ($k = 3$, stress $= 10.9$). Prior to ordination we also removed species observed five or less times to facilitate solution convergence in these permutational methods.

To associate sedge community composition with land-use history, current experimental management, tall fescue abundance, diversity/conservatism indices and mean wetland indicator status, we used the envfit function in the vegan package. Using site scores along NMDS axes as multivariate response variables, the envfit function measures the association between environmental variables and the relative location of sampling units in the ordination. Thus, envfit describes gradients of variation within ordination space representing the Bray-Curtis distance matrix.

We also compared beta diversity across land-use history and current experimental treatment groups using the vegan function betadisper, which measures the mean distance from points within a group to the group centroid within ordination space. Shorter distances represent higher homogeneity in community composition, as tighter groups span less area in ordination space. We used the Tukey HSD function for pair-wise *post-hoc* tests between groups.

Results
Overall abundance

Model comparison

Sedge abundance varied with year, land-use history and tall fescue abundance in the full LME regression model;

time-since-fire was not a statistically significant contributor to variation in the model. Likewise, these same variables were returned by the AIC selected model, which excluded time-since-fire. Fixed effect (independent predictor) variables in the full model explained 40% of variation in sedge abundance, while the selected model accounted for 39%. The full ($df = 14$, AIC $= 490.05$) and selected ($df = 11$, AIC $= 489.98$) models were not different in an analysis of variance ($P = 0.12$).

Each predictor variable performed similarly in the full and selected LME models. The only divergence was in whether the difference in sedge abundance between 2009 and 2010 was statistically significant (see below). Otherwise, results were consistent across both models, and *P*-values from the full model only are described here (complete results for both LME models and *post-hoc* Tukey pair-wise comparisons for each are included in App. S1).

Effects of individual variables

Sedge abundance increased throughout the study on each pasture. Compared to 2008, sedge abundance was higher in 2009 ($P < 0.01$) and 2010 ($P < 0.01$; Fig. 1). However, the significance of the increase in abundance from 2009 to 2010 varied among LME models, with the full model suggesting no statistically significant difference ($P = 0.53$), and the model returned by step-wise AIC model selection ($P = 0.01$) indicating that the increase was statistically significant. Across all tracts and all years, mean sedge cover was $26 \pm 2\%$ ($\pm$SE), which constituted $20 \pm 0.01\%$ of total plant cover; when only intact prairies were consid-
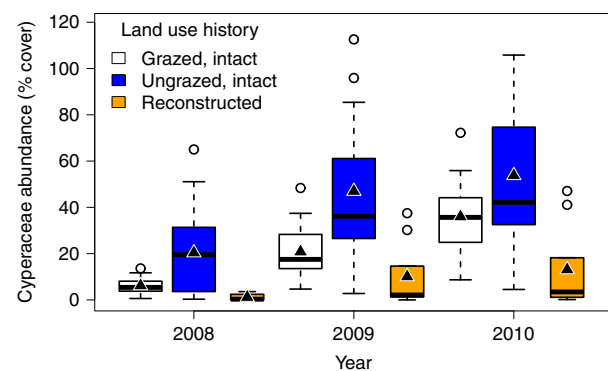

Fig. 1. Boxplot presents total abundance, measured as percent canopy cover, for 13 tallgrass prairie sedge communities, grouped by land use history and sampled over 3 yr. Whiskers extend to one interquartile range beyond the box, open circles beyond whiskers denote outlying values. Triangles denote group means. Overall, sedge abundance increased from 2008 to 2009 ($P < 0.01$) but did not differ between 2009 and 2010 ($P = 0.53$ in full linear mixed-effect regression model, but see Results). Sedge abundance was greater on previously-ungrazed intact prairie tracts than reconstructed prairie ($P < 0.01$) but did not differ among other groups.

ered, mean sedge cover increased to 30 ± 2% and total plant cover increased to 23 ± 0.01%.

Tracts with no known history of cultivation or grazing prior to our study had higher sedge abundance than reconstructed prairies ($P < 0.01$), but sedge abundance did not vary among these ungrazed intact tracts and previously grazed intact tracts ($P = 0.23$) nor among previously grazed intact tracts and reconstructed prairie ($P = 0.15$; Fig. 1). Time-since-fire was not statistically significant in any *post-hoc* pair-wise comparison ($P > 0.05$).

Tall fescue abundance had an inverse relationship with sedge abundance ($P = 0.02$), but model results suggest that land-use history, followed by annual increases from 2008 to 2010, best explain variation in sedge abundance on study tracts. Comparing beta coefficients indicates that tall fescue abundance contributes weakly to variation in sedge abundance ($|\beta| = 0.17$) compared to each pair-wise combination of land-use history ($|\beta| = 0.61, 0.48$ and 1.09) and sampling year ($|\beta| = 0.38, 0.55$ and 0.94).

Species richness, diversity and conservatism

We identified 21 sedge species across five genera (Table 2): *Carex* (16 spp.), *Scirpus* (2 spp.) and *Cyperus*, *Schoenoplectus* and *Scleria* (one species each). Tract-level observed species richness ranged from four to 13, with a mean of 8.5 ± 0.8. Table 1 reports observed and predicted species richness and diversity (1/D) by land-use history group. Observed species richness did not vary among land-use history groups ($P > 0.10$). Among experimental treatment groups, burn only tracts had higher species richness than both patch burn-grazed tracts ($P < 0.01$) and burned-and-grazed tracts ($P = 0.02$). Species richness among patch burn-grazed and burned-and-grazed tracts did not differ ($P = 0.61$). Diversity did not vary either among land-use history groups nor current experimental treatments (Table 1). Tall fescue abundance had no association with species richness, diversity or mean CoC ($P > 0.10$; App. S1).

Sedges spanned the range of conservatism values (Table 2), but mean CoC based on the Iowa and Missouri lists was 4.5 ± 0.2 and 5.0 ± 0.1, respectively. Neither mean Iowa CoC nor mean Missouri CoC varied among land-use history or current experimental treatment groups ($P > 0.20$; Table 2).

Sedge species were weighted towards wetland affinity (Table 1), with a mean WIS of −2.1 ± 0.2 on a scale of −5 (wetland obligates) to 5 (upland obligates). Five species were listed as wetland obligates and another four listed as facultative wetland (−4). Meanwhile, only four species were listed as upland obligates (5) and two as facultative upland (4). Six species were listed as facultative (0), meaning they occur in both wetlands and uplands.

Multivariate community composition

Ordination showed historical land use, current management, tall fescue abundance and measures of diversity, wetland indicator status and conservatism were associated with patterns of sedge community composition (Fig. 2). Sedge communities within tracts generally clustered together in ordination space, with wide variation among most tracts (Fig. 2b). Ordination of sedge communities correlated with tall fescue abundance ($R^2 = 0.61$, $P = 0.03$) and mean wetland indicator status ($R^2 = 0.16$, $P < 0.01$; Fig. 2b), as well as land-use history ($R^2 = 0.25$, $P < 0.01$; Fig. 2c) and current experimental treatment ($R^2 = 0.23$, $P = 0.01$; Fig. 2d). Despite correlation between mean CoC from the Iowa and Missouri lists ($R^2 = 0.47$), mean Iowa CoC correlated with the ordination ($R^2 = 0.44$, $P < 0.01$; Fig. 2b) while mean Missouri CoC did not ($R^2 = 0.02$, $P = 0.85$).

Species scoring to the left of the ordination plot generally had lower CoC (per the Iowa list) and lower WIS values than species towards the right of the plot (Fig. 2a). It is important to remember that the WIS ranges from −5 to 5, and thus higher WIS values – towards the left side of the plot – represent higher affinity for upland habitats, while species on the right are associated with wetlands.

Beta diversity varied across both land-use history and current experimental treatment grouping factors. Sedge community composition was significantly more homogeneous for reconstructed prairie than both previously grazed ($P < 0.01$) and previously ungrazed ($P < 0.01$), intact prairie, but within-group homogeneity did not vary among previously grazed and previously ungrazed intact prairie ($P = 0.59$). Across current experimental treatment groups, within-group homogeneity was higher for burn only tracts than both patch burn-grazed ($P = 0.04$) and burned-and-grazed ($P = 0.02$) tracts, but did not vary among either grazed treatment ($P = 0.88$).

Discussion

As expected, land-use history, current experimental management and tall fescue abundance were associated with patterns of sedge community composition. However, contrary to expectations, species richness, diversity and conservatism did not vary with land-use history or current management. These results have implications for the conservation and management of grassland in working landscapes.

Consistent with conventional wisdom on sedge habitat (Grime 1984; Fitter 2005), all observed species are native to the region, and only one infrequently observed species (*Cyperus esculentus*) is considered weedy (Bryson et al. 2008). And, despite our deliberate focus on upland

Table 2. List of 21 Cyperaceae (sedge) species sampled from 13 tallgrass prairie tracts over 3 yr, sorted alphabetically by genus and species within relative frequency of observation (local frequency). Primary scientific names follow the *Flora of North America North of Mexico*. Primary common names, scientific synonyms and wetland indicator status follow the USDA-PLANTS database. Common name synonyms (in parentheses) and CoC follow the Iowa State Herbarium at Iowa State University, Ames, Iowa, US; see Methods. For local frequency, rare species were observed on <5% of sampled tracts; uncommon species, 5–10% of tracts; occasional, 10–33% of tracts and common >33% of tracts.

Genus, Species author	Common name	Wetland indicator status	Local frequency	Coefficient of conservatism	
				Iowa	Missouri
Carex blanda Dewey	Eastern (common) woodland sedge	Facultative	Common	2	3
Schoenoplectus heterochaetus (Chase) Soják, syn. *Scirpus heterochaetus* Chase	Slender bulrush	Obligate wetland	Common	10	7
Carex brevior (Dewey) Mack. ex Lunell	Shortbeak (plains oval) sedge	Facultative	Occasional	4	4
Carex bushii Mack.	Bush's (long-scaled green) sedge	Facultative wetland	Occasional	0	3
Carex davisii Schwein. & Torr.	Davis' (awned graceful) sedge	Facultative	Occasional	4	4
Carex pellita Willd., syn. *Carex lasiocarpa* Ehrh. var. *americana* Fernald	Woolly sedge, syn. American woollyfruit sedge	Obligate wetland	Occasional	4	5
Carex retroflexa Muhl. ex Willd.	Reflexed (bent bracted) sedge	Obligate ipland	Occasional	5	4
Carex tetanica Schkuhr	Rigid (common stiff) sedge	Facultative wetland	Occasional	6	10
Carex vulpinoidea Michx.	(Brown) fox sedge	Obligate wetland	Occasional	3	4
Scirpus atrovirens Willdenow	Common (green) bulrush	Obligate wetland	Occasional	1	4
Carex cephalophora Muhl. ex Willd.	Oval-leaf (short-headed bracted) sedge	Facultative upland	Uncommon	5	5
Carex gravida L.H. Bailey	Heavy (long-awned bracted) sedge	Obligate upland	Uncommon	1	7
Carex hirsutella Mack.	Fuzzy wuzzy (hairy green) sedge	Facultative upland	Uncommon	4	n.a.
Carex bicknellii Britton	Bicknell's sedge	Facultative	Rare	10	8
Carex gracilescens Steud.	Slender looseflower (wood) sedge	Obligate upland	Rare	10	7
Carex molesta Mack. ex Bright	Troublesome (field oval) sedge	Facultative	Rare	2	4
Carex muehlenbergii Schkuhr ex Willd.	Muhlenberg's (sand bracted) sedge	Obligate upland	Rare	5	5
Carex scoparia Schkuhr ex Willd.	Broom (lance-fruited oval) sedge	Facultative wetland	Rare	5	4
Cyperus esculentus L.	Yellow nut grass	Facultative wetland	Rare	0	1
Scirpus georgianus Harper	Georgia bulrush	Obligate wetland	Rare	n.a.	n.a.
Scleria triglomerata Michaux	Tall nut grass (rush)	Facultative	Rare	5	7

landscape positions, there was a preponderance of species with wetland affinity (Lichvar 2013). Of course, species are often found beyond their 'obligate' habitats: one common sedge from these grasslands, *Carex blanda*, was previously described as a woodland species (Finch & Alexander 2011). Nevertheless, the association between wetland indicator status and community composition suggests a hydrological pattern among sampling locations and supports descriptions of fine niche resolution among sedge species along soil moisture gradients (e.g. Vellend et al. 2000). Prior work on spatial variability in tallgrass prairie plant community composition and productivity (Briggs & Knapp 1995; Baer et al. 2005) suggests soil depth might be particularly relevant in these grasslands.

The lack of difference in species richness, diversity or conservatism between historically ungrazed and historically severely grazed tracts runs contrary to grassland degradation theory. Literature describes a threshold of grazing severity, beyond which grazing negatively impacts vegetation through biotic degradation (Fuhlendorf et al. 2001; Briske et al. 2006), and below which grazing increases diversity by reducing dominance (Hickman et al. 2004). As the threshold depends on several variables including ecosystem productivity (Bakker et al. 2006), our results support the suggestion that these highly-productive mesic grasslands are quite resilient to severe grazing (McGranahan et al. 2012).

The connection between historical land use and current experimental management – both associated with patterns in sedge community composition – highlights the persistent role of land-use legacies and the challenges they pose to restoration and conservation (Bellemare et al. 2002; Foster et al. 2003). Previous work on non-sedge plant and invertebrate communities from these tracts (Debinski et al.
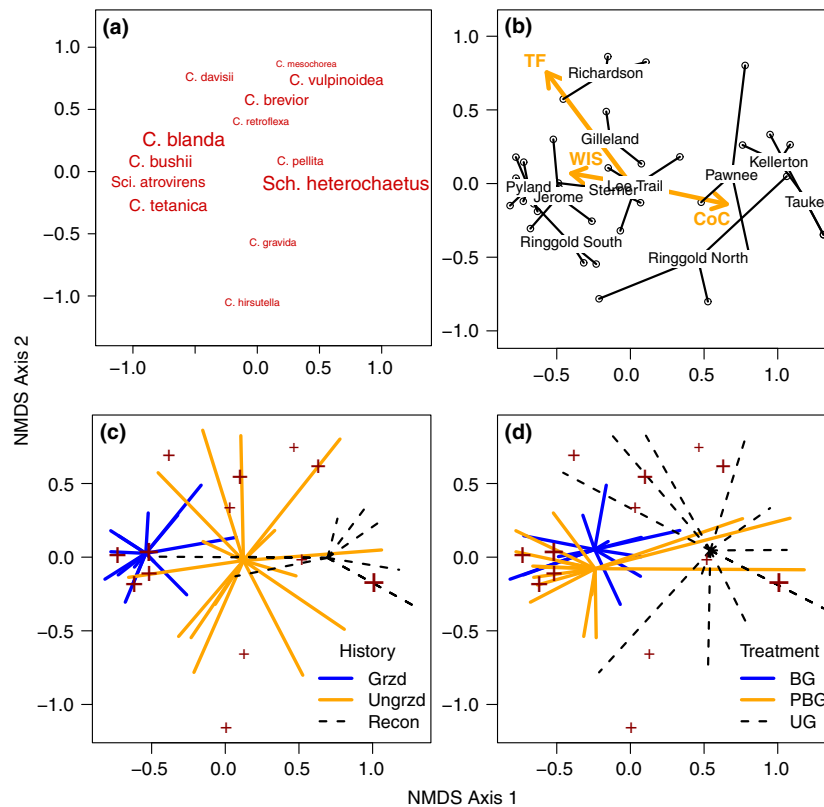
Fig. 2. Non-metric Multidimensional Scaling (NMDS; k = 3, stress = 10.9) of 13 tallgrass prairie sedge communities, presented as (**a**) Species scores, with font size proportional to frequency of observation; (**b**) Spider plots group sampled patches (site scores) by tract, with environmental vectors tall fescue abundance (TF: $R^2 = 0.61$, $P = 0.03$), mean Wetland Indicator Status (WIS: $R^2 = 0.16$, $P < 0.01$), and mean Iowa Coefficient of Conservatism (CoC: $R^2 = 0.44$, $P < 0.01$); (**c**) Spider plots group sampled patches (site scores) by land use history ($R^2 = 0.25$, $P < 0.01$), where 'Grzd' = Previously-grazed, intact prairie; 'Ungrzd' = Not previously-grazed, intact prairie; and 'Recon' = Reconstructed prairie; and (**d**) Spider plots group sampled patches (site scores) by current experimental treatment ($R^2 = 0.23$, $P = 0.01$), where 'BG' = Burned-grazed; 'PBG' = Patch burned-grazed; and 'UG' = Burned and ungrazed. NMDS based on a Bray-Curtis distance matrix of maximum sedge canopy cover for each of three patches per tract across three consecutive sampled years. In B, three Pyland tracts – Pyland North, South, and West – are plotted together for clarity. Symbols (+) in (**c**) and (**d**) correspond to species scores in (**a**).

2011; Moranz et al. 2012) suggests that legacies of historical land use contribute more to variation than current management, which we suspect also applies to sedge community composition. The statistical effect of current treatment is likely an artifact of experimental assignment: previously ungrazed tracts tended to remain ungrazed under the experimental design, while previously grazed tracts were assigned to grazing treatments. Indeed, Fig. 2c shows higher separation among all three land-use history groups, while Fig. 2d shows considerable overlap between both current grazing treatments and previously grazed tracts. These patterns underscore the importance of (i) considering the effect of previous land use and (ii) monitoring the effect of restoration efforts through time.

As predicted, sedge community composition on reconstructed prairie differed from intact grassland, but the similarity in species richness, diversity and conservatism between reconstructed and intact grassland was contrary

to both our expectations and existing literature on tallgrass prairie restoration (Galatowitsch & van der Valk 1996; Polley et al. 2005). The main difference between the two prairie types was sedge abundance, which was lower in reconstructed prairie (Fig. 1). Two interesting patterns occur within the reconstructed group: Kellerton and Tauke – both tilled and re-seeded with native species – had much lower sedge abundance than Sterner, where restoration consisted of seeding native species into the existing pasture matrix. But higher sedge abundance does not alone indicate Sterner is less degraded than the intensively managed tracts: note that in ordination space (Fig. 2b) Sterner groups more closely with degraded tracts (e.g. Gilleland, Jerome and Pylands) while Kellerton and Tauke group near Pawnee and Ringgold North, both high-quality prairie (McGranahan et al. 2013). Unfortunately we lack replication among different types of reconstructed prairie, but these results suggest that although reconstructed prairie

vegetation does differ from that of intact grassland, differences in community composition do not necessarily relate to differences in floristic quality.

The pattern in conservatism is relevant to grassland conservation, as coefficients of conservatism are used to evaluate the floristic quality of plant communities, determine biodiversity conservation potential and prioritize conservation land acquisition (Jalava & Godschalk 1998; Jog et al. 2006). In a multivariate analysis of prairie communities ranging from undegraded remnants to reconstructions, mean CoC was a robust metric of floristic quality (Taft et al. 2006). The relationship between mean CoC and plant community composition in our multivariate analysis supports the use of floristic quality indices over standard diversity indices but does not support the use of either type of index to discern disturbance history. Overall, our results underscore the value of multivariate, species-specific community data over simple diversity measures (Wilsey et al. 2005).

Tall fescue abundance was associated with sedge community composition but was not related to species richness, diversity or conservatism. This runs counter to previous work from these grasslands that found native, non-sedge plant species richness declines with tall fescue abundance (McGranahan et al. 2012). However, our data do support evidence that tall fescue abundance is an important contributor to plant community composition (McGranahan et al. 2013). It is clear that the sedge communities of tracts with high tall fescue abundance differ in composition from tracts with less tall fescue, especially among historically ungrazed tracts, in which high within-group heterogeneity in community composition (beta diversity) follows the gradient of tall fescue abundance (Fig. 2b,c). But whether tall fescue excludes certain sedges or whether tall fescue abundance and sedge community composition share some indirect response to previous management cannot be determined.

The high abundance of sedge biomass in this working landscape translates to a major forage resource for grazing. Across most tracts (with the exception of Tauke and Kellerton), sedges composed a substantial portion of the available forage, especially after the first year of the study. Sedges were approximately one quarter of total plant cover on intact grassland, typical for tallgrass prairie (Coppedge et al. 1998b). Other work shows above-ground plant biomass – as well as community composition – is affected by annual variation in precipitation (Gibson & Hulbert 1987; Coppedge et al. 1998a; Gross & Romo 2009), which likely explains year-to-year variation in our data. The 3 yr prior to our study averaged less rainfall than the 3-yr study period – 952 mm v 1387 mm, respectively (IEM 2011) – and the increase in sedge abundance from 2008 to 2009 is likely attributable to plant recovery from drought. While tall fescue had a statistically significant negative association with sedge abundance, which might suggest competition between these two components of the cool-season graminoid community, our data do not indicate that tall fescue is a major factor in reducing sedge abundance, and it is unlikely that they compete.

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References

Allessio Leck, M. & Schütz, W. 2005. Regeneration of Cyperaceae, with particular reference to seed ecology and seed banks. *Perspectives in Plant Ecology, Evolution and Systematics* 7: 95–133.

Anderson, H.G. & Bailey, A.W. 1980. Effects of annual burning on grassland in the aspen parkland of east-central Alberta. *Canadian Journal of Botany* 58: 985–996.

Baer, S.G., Collins, S.L., Blair, J.M., Knapp, A.K. & Fiedler, A.K. 2005. Soil heterogeneity effects on tallgrass prairie community heterogeneity: an application of ecological theory to restoration ecology. *Restoration Ecology* 13: 413–424.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G. & Knops, J.M.H. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9: 780–788.

Bellemare, J., Motzkin, G. & Foster, D.R. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography* 29: 1401–1420.

Bowles, M.L. & Jones, M.D. 2013. Repeated burning of eastern tallgrass prairie increases richness and diversity, stabilizing late successional vegetation. *Ecological Applications* 23: 464–478.

Briggs, J.M. & Knapp, A.K. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of above-ground biomass. *American Journal of Botany* 82: 1024–1030.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F. 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology & Management* 59: 225–236.

Bryson, C.T., Carter, R., Naczi, R. & Ford, B. 2008. The significance of Cyperaceae as weeds. In: Naszi, R.F.C. &

Ford, B.A. (eds.) *Sedges: uses, diversity, and systematics of the Cyperaceae*, pp. 15–101. Missouri Botanical Garden Press, St. Louis, MO, US.

Clark, P.E. 2003. Date and plant community effects on elk sedge forage quality. *Journal of Range Management* 56: 21–26.

Collins, S.L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68: 1243–1250.

Collins, S.L. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology* 73: 2001–2006.

Collins, S.L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *The American Naturalist* 155: 311–325.

Collins, S.L. & Smith, M.D. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87: 2058–2067.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745.

Coppedge, B.R., Engle, D.M., Toepfer, C.S. & Shaw, J.H. 1998a. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology* 139: 235–246.

Coppedge, B.R., Leslie, D.M. Jr & Shaw, J.H. 1998b. Botanical composition of bison diets on tallgrass prairie in Oklahoma. *Journal of Range Management* 51: 379–382.

Cramer, V.A., Hobbs, R.J. & Standish, R.J. 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution* 23: 104–112.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33: 43–64.

Debinski, D.M., Moranz, R.A., Delaney, J.T., Miller, J.R., Engle, D.M., Winkler, L.B., McGranahan, D.A., Barney, R.J., Trager, J.C., Stephenson, A.L. & Gillespie, M.K. 2011. A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. *Ecosphere* 2: art131.

Enders, C.K. & Tofighi, D. 2007. Centering predictor variables in cross-sectional multilevel models: a new look at an old issue. *Psychological Methods* 12: 121–138.

Finch, D.D. & Alexander, H.M. 2011. Variation in plant distributions, plant traits and disease levels across a woodland/grassland ecotone. *The American Midland Naturalist* 166: 309–324.

Fitter, A.H. 2005. Darkness visible: reflections on underground ecology. *Journal of Ecology* 93: 231–243.

Flora of North America Editorial Committee. 1993. *Flora of North America (North of Mexico)*. Oxford University Press, vol. 3. New York, NY, US.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D. & Knapp, A. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53: 77–88.

Fraterrigo, J.M., Turner, M.G., Pearson, S.M. & Dixon, P. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. *Ecological Monographs* 75: 215–230.

Fuhlendorf, S.D., Briske, D.D. & Smeins, F.E. 2001. Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. *Applied Vegetation Science* 4: 177–188.

Galatowitsch, S.M. & van der Valk, A.G. 1996. The vegetation of restored and natural prairie wetlands. *Ecological Applications* 6: 102–112.

Gibson, D.J. & Hulbert, L.C. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72: 175–185.

Gignac, L.D., Gauthier, R., Rochefort, L. & Bubier, J. 2004. Distribution and habitat niches of 37 peatland Cyperaceae species across a broad geographic range in Canada. *Canadian Journal of Botany* 82: 1292–1313.

Goetghebeur, P. 1998. Cyperaceae. In: Kubitzki, K. (ed.) *Flower plants monocotyledons*, pp. 141–190. Springer, Berlin, DE.

Grime, J. 1984. The ecology of species, families and communities of the contemporary British flora. *New Phytologist* 98: 15–33.

Gross, D.V. & Romo, J.T. 2009. Temporal changes in species composition in Fescue Prairie: relationships with burning history, time of burning, and environmental conditions. *Plant Ecology* 208: 137–153.

Harvey, L. & Fortin, D. 2013. Spatial heterogeneity in the strength of plant–herbivore interactions under predation risk: the tale of bison foraging in wolf country. *PLoS ONE* 8: e73324.

Hickman, K.R., Hartnett, D.C., Cochran, R.C. & Owensby, C.E. 2004. Grazing management effects on plant species diversity in tallgrass prairie. *Journal of Range Management* 57: 58–65.

Holechek, J.L., Vavra, M., Skovlin, J. & Krueger, W.C. 1982. Cattle diets in the Blue Mountains of Oregon. II Forests. *Journal of Range Management* 35: 239–242.

Houseal, G. & Smith, D.D. 2010. Upland sedge (*Carex* spp.) propagation for seed increase. *Proceedings of the North America Prairie Conference* 21: 132–138.

IEM. 2011. Iowa Environmental Mesonet, Iowa State University Department of Agronomy: Lamoni, IA. Available from http://mesonet.agron.iastate.edu/climodat/index.phtml?station=IA4585&report=17 (accessed 31 May 2011).

Jalava, J. & Godschalk, H. 1998. Priority sites for conservation action in the Niagara Escarpment Biosphere Reserve. Parks Protected Areas Research Ontario 1998 Proceedings of the Parks Research Forum Ontario, PRFO 1998 Annual General Meeting, February 5–6 1998 Peterb Ont. pp. 201. Parks Research Forum of Ontario, OT, CA.

Jog, S., Kindscher, K., Questad, E., Foster, B. & Loring, H. 2006. Floristic quality as an indicator of native species diversity in managed grasslands. *Natural Areas Journal* 26: 149–167.

Kettenring, K.M. 2006. Effect of light on seed germination of eight wetland *Carex* species. *Annals of Botany* 98: 869–874.

Kettenring, K.M. & Galatowitsch, S.M. 2011. *Carex* seedling emergence in restored and natural prairie wetlands. *Wetlands* 31: 273–281.

Lichvar, R.W. 2013. The National Wetland Plant List: 2013 wetland ratings. *Phytoneuron* 2013–49: 1–241.

McGranahan, D.A., Engle, D.M., Wilsey, B.J., Fuhlendorf, S.D., Miller, J.R. & Debinski, D.M. 2012. Grazing and an

invasive grass confound spatial pattern of exotic and native grassland plant species richness. *Basic and Applied Ecology* 13: 654–662.

McGranahan, D., Engle, D., Fuhlendorf, S., Miller, J. & Debinski, D. 2013. Multivariate analysis of rangeland vegetation and soil organic carbon describes degradation, informs restoration and conservation. *Land* 2: 328–350.

Miller, J.R., Morton, L.W., Engle, D.M., Debinski, D.M. & Harr, R.N. 2012. Nature reserves as catalysts for landscape change. *Frontiers in Ecology and the Environment* 10: 144–152.

Moranz, R.A., Debinski, D.M., McGranahan, D.A., Engle, D.M. & Miller, J.R. 2012. Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. *Biodiversity and Conservation* 21: 2719–2746.

Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.

Palmer, M.W. 1990. The estimation of species richness by extrapolation. *Ecology* 71: 1195–1198.

Polley, H.W., Derner, J.D. & Wilsey, B.J. 2005. Patterns of plant species diversity in remnant and restored tallgrass prairies. *Restoration Ecology* 13: 480–487.

Rudgers, J.A., Mattingly, W.B. & Koslow, J.M. 2005. Mutualistic fungus promotes plant invasion into diverse communities. *Oecologia* 144: 463–471.

Shay, J., Kunec, D. & Dyck, B. 2001. Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Manitoba. *Plant Ecology* 155: 157–167.

Ssegawa, P., Kakudidi, E., Muasya, M. & Kalema, J. 2004. Diversity and distribution of sedges on multivariate environmental gradients. *African Journal of Ecology* 42: 21–33.

Stohlgren, T.J., Bull, A. & Otsuki, Y. 1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. *Journal of Range Management* 51: 164–172.

Swink, F. & Wilhelm, G. 1994. *Plants of the Chicago region*. Indiana Academy of Science Indianapolis, Indianapolis, IN, US.

Taft, J.B., Hauser, C. & Robertson, K.R. 2006. Estimating floristic integrity in tallgrass prairie. *Biological Conservation* 131: 42–51.

USDA-NRCS. 2010. Web Soil Survey data for Ringgold County, Iowa Natural Resource Conservation Service, United States Department of Agriculture. Available from http://websoil-survey.nrcs.usda.gov (accessed 25 February 2011).

Van der Valk, A.G. 2013. Seed banks of drained floodplain, drained palustrine, and undrained wetlands in Iowa, USA. *Wetlands* 33: 183–190.

Vellend, M., Lechowicz, M.J. & Waterway, M.J. 2000. Environmental distribution of four *Carex* species (Cyperaceae) in an old-growth forest. *American Journal of Botany* 87: 1507–1516.

White, R.S. & Currie, P.O. 1983. Prescribed burning in the Northern Great Plains: yield and cover responses of 3 forage species in the mixed grass prairie. *Journal of Range Management* 36: 179–183.

Wilsey, B.J., Chalcraft, D.R., Bowles, C.M. & Willig, M.R. 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology* 86: 1178–1184.

Supporting Information

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

Appendix S1. Complete R code for analysis + results.
Appendix S2. Sedge abundance and community data.