

An assessment of grassland restoration success using species diversity components

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Summary

1. We do not know which aspects of community structure and ecosystem processes are restorable for most ecosystems, yet this information is crucial for achieving successful restoration.
2. We quantified three success criteria for 8–10-year-old grassland plantings in large-scale tallgrass prairie restoration (reconstruction) sites relative to three nearby prairie remnant sites. The restoration sites included management of native ungulates and fire, important regulators of diversity and patchiness in intact grasslands. These have not been incorporated simultaneously into previous studies of restoration success.
3. We used the additive partitioning model of diversity, where α is neighbourhood (quadrat) scale diversity, β is accumulation of species diversity across neighbourhoods, and γ is total diversity. We decomposed α into richness and evenness to determine if both were equally restored.
4. The proportion of exotic biomass was similar between the restoration and remnant sites, but the proportion of exotic species and above-ground net primary productivity remained between two and four times higher in the restoration sites.
5. Alpha diversity (Simpson's $1/D$) and richness (S) values were exceptionally high in remnant sites, and approximately twice those of the restoration sites. Alpha evenness was similar between the restoration and remnant sites.
6. Distance *per se* between quadrats was not related to diversity after accumulated quadrat area was taken into account. Therefore, we may be able to use the additive partitioning model of diversity in areas that differ in size, at least at the scale of this study.
7. Contrary to our original predictions, the proportion of β diversity ($1 - D$) was approximately twice as high in the restoration sites than in remnant sites, possibly because patches of individual species were larger in the restoration.
8. *Synthesis and applications.* We have shown that current restoration methods are unable to restore plant diversity in tallgrass prairie. Grassland restoration will be improved if the number of species that co-exist can be increased. New, local-scale restoration techniques are needed to replicate the high levels of diversity observed in tallgrass prairie remnant sites.

Key-words: beta diversity, evenness, Iowa, net primary productivity, restoration, richness, tallgrass prairie

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Introduction

An increasingly common goal of ecosystem restoration is to replicate the high levels of plant species, trait and

functional group diversity found in remnant sites (Pywell *et al.* 2003; Smith *et al.* 2003). Species diversity has two components (Stirling & Wilsey 2001): richness (number of species) and evenness (how evenly abundance or biomass is distributed among species). High evenness can increase invasion resistance, total and below-ground productivity, and can reduce local plant extinction rates (Wilsey & Potvin 2000; Wilsey & Polley 2002, 2004; Smith *et al.* 2004). Species richness has

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been found to be lower in grassland restoration sites in comparison with remnant sites (Kindscher & Tieszen 1998; Polley, Derner & Wilsey, in press) and, in contrast to expectations, richness has even decreased with time since restoration (Sluis 2002). Previous comparisons between restoration and remnant sites have revealed no differences in evenness (Kindscher & Tieszen 1998), although such a finding may depend on the scale of study (Polley, Derner & Wilsey, in press). These examples of restoration, however, have not included impact of grazing, which has been known to increase evenness in intact systems (McNaughton 1979; Hartnett, Hickman & Walter 1996).

Restoring spatial components of diversity is rarely recognized as a goal in restoration, even though it is an integral component of ecological systems (Menge & Olson 1990; Baer *et al.* 2003; Baer *et al.* 2004). Native ungulate activities in intact grasslands can increase β diversity (patchiness) of plant communities as a result of spatially variable grazing patterns, urination and wallowing (Knapp *et al.* 1999).

Restoring community structure (e.g. species composition and diversity) and ecosystem process rates are usually listed as two main objectives of restoration and vegetation improvement (Palmer, Ambrose & Poff 1997; Lockwood & Pimm 1999; Moore, Covington & Fule 1999; Smith *et al.* 2000). However, we must develop criteria with which to quantitatively measure success if we are to develop more successful restorations (Palmer *et al.* 2005). We propose that restoration success should quantify how well four main ecosystem attributes have been restored (modified from Bradshaw 1996 and Hobbs & Norton 1996):

1. the proportion of native species;
2. ecosystem processes (e.g. net primary productivity and nutrient cycling);
3. plant diversity at all spatial scales;
4. animal and microbial diversity at all spatial scales.

In this study, we focused on the first three criteria because primary productivity and vegetative habitat components usually have to be restored before animals are reintroduced (Merrill *et al.* 1999). Our objective was to quantify success of grassland plantings within a large tallgrass prairie restoration (reconstruction) project in Iowa, USA, compared with three nearby remnant prairies. Tallgrass prairie is an appropriate ecosystem in which to evaluate restoration success because it is one of the most endangered ecosystems, with 82–99% of North American tallgrass prairie now converted (Samson & Knopf 1994), and its diversity and productivity can be measured relatively easily. Our study provides a valuable perspective on tallgrass restoration as plantings were located in the largest tallgrass prairie restoration in the USA, and the restoration sites included both fire (Cottam & Wilson 1966; Sluis 2002; Polley, Derner & Wilsey, in press) and native ungulate grazing, which are two of the most critical regulators of intact grassland structure (Collins *et al.* 1998; Knapp *et al.* 1999; Copeland, Sluis & Howe 2002).

Materials and methods

RESTORATION STUDY SITE

Neal Smith National Wildlife Refuge contains the largest prairie restoration (reconstruction) project in the USA. The objectives of the refuge staff are to use locally collected seeds combined with prescribed fire and grazing by native ungulates to restore tallgrass prairie. The restoration site was established in 1991 in southern Iowa, USA (41°33'N, 93°17'W), and is currently 2104 ha, of which approximately 1200 have been seeded with tallgrass prairie species. Bison and elk were reintroduced to a 303-ha enclosure in 1996 and 1998, respectively, which is where our study took place. Prior land use included corn *Zea mays* L. and soybean *Glycine max* (L.) Merr rotations and a few scattered pastures, and crops were probably fertilized on an annual or biannual basis. There were 20 different plantings in this area (mean size 14 ha), and each was seeded with separate bulk mixes collected from local prairie remnant sites. Management practices included yearly spring burning, which is a common practice at the outset of restoration projects (Packard & Mutel 1997; Copeland, Sluis & Howe 2002), and occasional mowing to control exotic species (P. Drobney, personal communication). However, none of our sites was burned or mowed during the years (2002 and 2003) of our sampling.

Three nearby tallgrass prairie remnant sites were selected for a range of reference sites based on their proximity to the restoration area (A.C. Morris = 36 km, Rolling Thunder = 51 km, Sheeder = 109 km), similar soil types (mollisols) and, most importantly, because they had never been ploughed or overseeded with forage grasses. The A.C. Morris Prairie (41°47'N, 92°58'W) is an 8-ha remnant that was grazed before 1977; Rolling Thunder Prairie (41°12'N, 93°39'W) is a 50-ha remnant that was grazed by cattle before 1983 (Herzberg & Pearson 2001); and Sheeder Prairie (41°41'N, 94°35'W) is a 10-ha remnant that was cut for hay and possibly grazed by cattle prior to 1968 (Herzberg & Pearson 2001). Current management of remnant sites includes prescribed burning every few years. Annual precipitation at all sites has a unimodal distribution, with peak precipitation in May–June, and averages approximately 882 mm year⁻¹.

SAMPLING DESIGN

To standardize our sampling, we selected eight plantings within the enclosure at Neal Smith that were seeded between 1994 and 1996 on formerly cropped areas. Paired 6 × 8-m plots (left and right) were established in each of the eight plantings in the restoration. Plots were paired because of their utilization in a separate study and pairing was taken into account in statistical analyses as explained below. By request of refuge staff, restoration plots were kept out of view of visitors when possible, and this precluded completely

random locations. The C_3 grass *Elymus canadensis* was added to the mix (6.7 kg ha^{-1}) as a cover crop for plantings in the northern half of the site. Therefore, the sampling pattern in restored plantings resulted in four paired plots (eight total) in which *E. canadensis* was included in the seed mixes and four paired plots in which it was not. Eight plots of $6 \times 8 \text{ m}$ were also established within each remnant using randomly sampled locations.

SAMPLING METHODS

Above-ground biomass was clipped to 2 cm in a $40 \times 100\text{-cm}$ quadrat within each plot at each site, and surface litter was collected during three periods: 24 September–2 October 2002, 27 May–9 June 2003 and 19–26 August 2003. Early and late sampling dates were used to ensure sampling of both early and late-growing species. We sorted above-ground plant material from each plot into live (at least some green present) and standing dead (green absent) mass, and then sorted live material by species. Biomass, standing dead mass and litter were dried to constant mass (for 48 h) at 65°C and weighed.

The proportions of exotic biomass and species (exotic/total) were calculated at the quadrat level. Plant species were designated as native or exotic based on Eilers & Roosa (1994), with the exception of *Rubus ablatus*, which was designated as native using Widrlechner (1998).

Above-ground net primary productivity (NPP) was estimated with peak biomass, and consumed biomass was added to peak biomass at the restoration sites for 2003. Consumption was estimated using the temporary enclosure technique of McNaughton, Milchunas & Frank (1996).

SPECIES DIVERSITY

To quantify spatial aspects of diversity, we partitioned it into α and β components (Whittaker 1960; Lande 1996), where α was neighbourhood (quadrat)-scale and γ was prairie-scale diversity. We used the additive partitioning model of diversity ($\beta = \gamma - \alpha$) because γ , α and β have the same units and thus can be compared directly (Lande 1996; Crist *et al.* 2003). Alpha diversity was calculated using Simpson's diversity index $1/D$ (hereafter referred to as Simpson's diversity), where $D = \sum p_i^2$, with p_i being the relative biomass of each species i . Alpha diversity was then decomposed into richness (S) and evenness (E) components (Buzas & Hayek 1996; Smith & Wilson 1996). Evenness was calculated as $E = 1/D/S$ because this index is mathematically independent of richness (Smith & Wilson 1996). Gamma (γ) diversity was partitioned into α and β using the $1 - D$ form of Simpson's index (hereafter referred to as $1 - D$) and S because of their desirable statistical properties when additively partitioned (Lande 1996).

Sites differed in size, and thus plots differed in their distance from one another within a site. Varying dis-

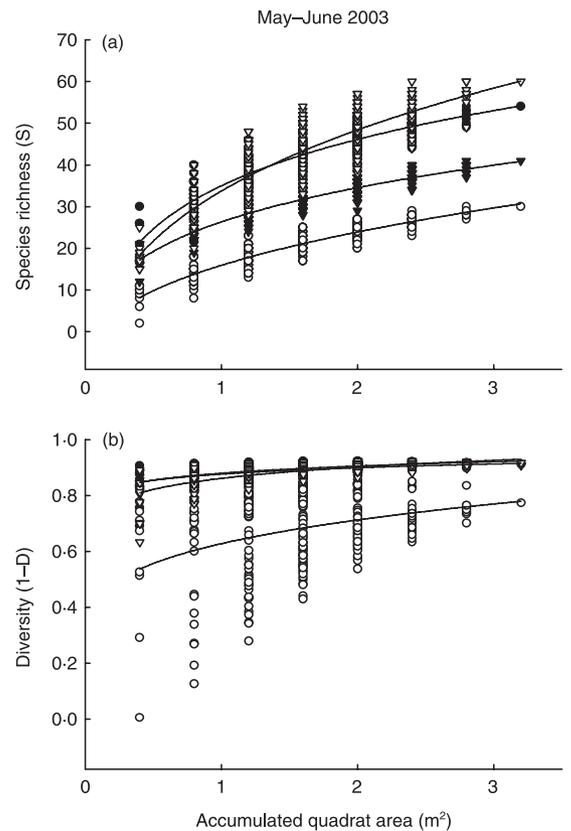


Fig. 1. Example of all possible combinations of quadrats for (a) species richness (S) and (b) diversity ($1 - D$) with accumulated quadrat area for the restoration sites (Neal Smith National Wildlife Refuge, open circles) and three remnant prairie sites (Sheeder, open triangles; A.C. Morris, solid circles; Rolling Thunder, closed triangles). Residuals of these plots were unrelated to mean distance between plots, suggesting that distance *per se* had no effect on diversity.

tances between quadrats could potentially complicate comparisons of sites. To determine if distance between quadrats was related to diversity above and beyond the effect of accumulated quadrat area, we plotted all possible combinations of S and $1 - D$ against area, and then estimated the best-fitting curve (a three-parameter power curve; $y = y_0 + ax^b$) to data from each site (Fig. 1). We then tested if residuals from these plots were related to mean distance (measured using ArcView GIS) between quadrats with linear regressions.

STATISTICAL ANALYSES

We performed repeated-measures ANOVA for each variable except proportion of β diversity, because an appropriate test of between-group differences has not been developed. For proportion of β we took the conservative approach of assigning significance if the restoration site mean was outside the range of remnant sites. Paired plots were more similar (Bray-Curtis similarity measure; Krebs 1998) to each other than to other plots within the restoration, indicating that pairs were not completely independent of each other. Therefore, we adopted the conservative approach of using the degrees

of freedom (7) associated with one plot from each pair to test restoration vs. remnant effects. We did not average across pairs so that they would be more comparable with the sampling design in each remnant. Above-ground NPP, litter and standing dead mass were ln-transformed before analyses to improve normality. A priori contrasts were used to test the hypothesis that the restoration sites differed from the three remnant sites combined.

In a separate analysis using the restoration site only, we tested for differences between the *E. canadensis* cover crop treatment using repeated-measures ANCOVA (the distance from Walnut Creek was a covariate because the creek potentially carried exotic seeds). In this analysis, we averaged across paired plots within each planting. We tested proportion of exotic species and biomass, number of exotic species and α diversity (S, E and 1/D).

Results

PROPORTION OF EXOTICS

Restored plantings were dominated by the native grasses *Andropogon gerardii* and *Sorghastrum nutans* or the forb *Helianthus grosseserratus* (Table 1). The proportion of exotics per 0.4 m² was not consistently greater in the restoration sites and depended on whether the proportion of species or proportion of biomass was used (Table 2 and Fig. 2). The proportion of exotic species was between 236% and 413% higher in the restoration than in remnant sites (Fig. 2a). The absolute number of exotic species was also significantly greater in the restoration sites (Table 2). However, the proportion of exotic biomass was not significantly different between the restoration and remnant sites (Table 2 and Fig. 2b). The exotic *Poa pratensis* made up a large portion of biomass in remnant sites and accounted for the lack of a difference (Table 1). Across sites, the proportion of exotic biomass was greatest in May–June 2003 (Table 2 and Fig. 2b).

At the restoration sites, the proportion of exotic species was significantly greater in plantings without the cover crop treatment ($F_{1,5} = 8.99$, $P = 0.03$; mean across times for cover crop = 0.18; no cover crop = 0.45). The cover crop treatment had no effect on exotic biomass and absolute number of exotic species ($F_{1,5} = 0.06$, $P = 0.81$; $F_{1,5} = 2.02$, $P = 0.21$, respectively; means of 0.12 and 2.3 for cover crop and 0.17 and 3.5 for no cover crop for biomass and exotic species, respectively).

ECOSYSTEM VARIABLES

Above-ground net primary productivity (g m⁻² year⁻¹) without consumption added was similar between the restoration and remnant sites for 2002 and 2003 ($F_{1,28} = 0$, $P > 0.1$, $F_{1,28} = 1.18$, $P > 0.1$) but it was significantly greater at the restoration sites when we included estimates of consumption in 2003 ($F_{1,28} = 16.84$, $P < 0.01$; Table 3). Litter mass was significantly greater in the restoration sites in 2003 (time–contrast inter-

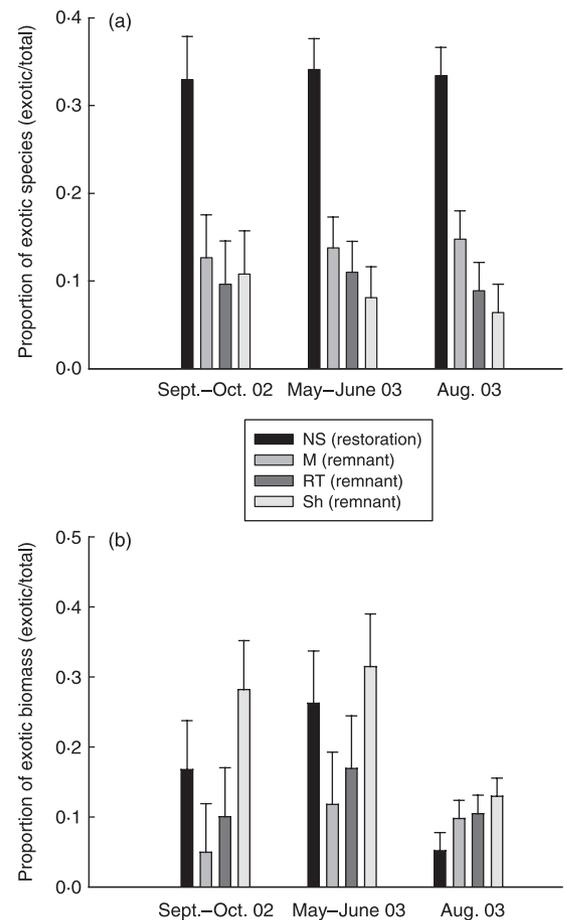


Fig. 2. Proportion of (a) exotic species and (b) exotic biomass in a large tallgrass prairie restoration site (Neal Smith National Wildlife Refuge, NS) and three remnant prairie sites. A.C. Morris, M; Rolling Thunder, RT; Sheeder, Sh.

action, $F_{2,56} = 5.21$, $P < 0.01$) whereas standing dead mass did not differ ($F_{1,28} = 2.31$, $P = 0.14$; Table 1).

ALPHA DIVERSITY

Simpson's diversity and richness at the plot scale were significantly greater in remnant sites, but α evenness did not differ between the restoration and remnant sites (Table 2 and Fig. 3). Simpson's diversity and richness in the restoration sites were 43–47% and 43–58% that of remnant sites (Fig. 3). Temporal variation in species richness differed between the restoration and remnant sites, with an increase through time in restoration sites, while remnant sites peaked in May–June 2003 (time–contrast interaction; Table 2 and Fig. 3a). Alpha richness was greater in the remnant sites in spring because of the greater number of rare vernal forbs that were absent from the restoration sites.

Simpson's diversity and evenness were significantly greater in the cover crop sites ($F_{1,5} = 36.33$, $P < 0.01$; $F_{1,5} = 7.47$, $P = 0.04$; means of 3.9 and 0.4 for cover crop and 1.2 and 0.2 for no cover crop for Simpson's diversity and evenness, respectively). Species richness

Table 1. Mean relative biomass (percentage of total) and relative frequency of the most common species in 8–10-year-old plantings within a large-scale tallgrass prairie restoration site (Neal Smith National Wildlife Refuge, NS) and three remnant prairie sites (A.C. Morris, M; Rolling Thunder, RT; Sheeder, Sh). Exotic species are in bold, and nomenclature follows Eilers & Roosa (1994). Mean standing dead mass and litter (g m⁻²) (SE) are included at the end of each site list

Scientific name	Relative biomass (SE)				Mean relative frequency
	September–October 2002	May–June 2003	August 2003	Mean	
NS					
<i>Andropogon gerardii</i>	54.4 (12.1)	32.8 (10.4)	41.8 (10.6)	43.0	0.96
<i>Sorghastrum nutans</i>	18.1 (9.1)	5.3 (4.3)	8.7 (4.5)	10.7	0.38
<i>Phalaris arundinacea</i>	0 (0)	12.5 (12.5)	11.2 (11.2)	7.9	0.08
<i>Helianthus grosseserratus</i>	3.3 (3.3)	9.1 (6.2)	11.2 (10.2)	7.9	0.21
<i>Poa pratensis</i>	13.4 (9.0)	8.6 (8.5)	0.5 (0.3)	7.5	0.29
Standing dead mass	331.4 (32.1)	270 (55)	303.9 (49.5)		
Litter	164.4 (64.8)	193.6 (29.2)	303.3 (38.3)		
M					
<i>Carex</i> spp.	8.2 (1.5)	24.1 (3.3)	9.0 (1.6)	13.8	1
<i>Schizachyrium scoparium</i>	20.0 (10.0)	6.7 (5.7)	11.4 (8.1)	12.7	0.54
<i>Helianthus grosseserratus</i>	11.0 (5.5)	7.3 (2.9)	11.4 (4.9)	9.9	0.54
<i>Andropogon gerardii</i>	10.8 (10.5)	5.4 (4.8)	10.3 (10.2)	8.8	0.29
<i>Aster ericoides</i>	7.3 (4.8)	8.2 (3.1)	8.8 (2.9)	8.1	0.83
<i>Poa pratensis</i>	3.7 (1.2)	7.9 (2.1)	6.5 (1.7)	6.1	0.92
<i>Monarda fistulosa</i>	9.3 (5.0)	3.2 (1.3)	2.3 (1.1)	4.9	0.71
<i>Ratibida pinnata</i>	3.6 (1.6)	4.3 (1.4)	4.9 (2.4)	4.3	0.83
<i>Solidago canadensis</i>	3.4 (3.4)	3.2 (1.9)	4.2 (2.7)	3.6	0.29
<i>Rosa</i> sp.	2.8 (1.3)	3.8 (0.1)	4.2 (1.7)	3.6	0.96
Standing dead mass	120.9 (32.1)	220.5 (55.0)	259.2 (49.5)		
Litter	120 (64.8)	91.9 (29.2)	82.9 (38.3)		
RT					
<i>Sorghastrum nutans</i>	23.3 (6.7)	7.1 (1.5)	18.2 (3.2)	16.2	1
<i>Schizachyrium scoparium</i>	16.9 (3.8)	13.9 (3.3)	11.5 (4.0)	14.1	0.92
<i>Andropogon gerardii</i>	9.5 (6.1)	8.7 (3.6)	18.3 (7.8)	12.2	0.63
<i>Solidago canadensis</i>	20.9 (9.4)	7.0 (1.9)	5.3 (2.5)	11.1	0.75
<i>Poa pratensis</i>	7.2 (1.3)	14.6 (1.7)	8.3 (1.0)	10.0	1
<i>Carex</i> spp.	3.5 (0.7)	13.7 (2.4)	4.3 (0.7)	7.1	1
<i>Rubus ablatus</i>	3.0 (1.6)	9.1 (2.7)	5.0 (2.6)	5.7	0.63
Standing dead mass	108.6 (32.1)	254.7 (55.0)	291 (49.5)		
Litter	213.2 (64.8)	102 (29.2)	71.8 (38.3)		
Sh					
<i>Poa pratensis</i>	17.5 (6.3)	22.2 (6.0)	9.7 (2.9)	16.5	1
<i>Solidago gigantea</i>	6.7 (5.1)	14.6 (5.7)	9.0 (5.5)	10.1	0.42
<i>Helianthus rigidus</i>	9.5 (5.1)	7.1 (3.9)	7.9 (2.4)	8.2	0.63
<i>Andropogon gerardii</i>	4.4 (3.4)	4.2 (2.0)	9.0 (3.3)	5.9	0.58
<i>Melilotus alba</i>	10.5 (7.5)	6.9 (6.3)	0 (0)	5.8	0.17
<i>Monarda fistulosa</i>	5.5 (2.9)	1.2 (0.8)	7.4 (5.0)	4.7	0.50
<i>Ceanothus americanus</i>	0.6 (0.5)	1.2 (1.2)	9.2 (6.1)	3.7	0.21
<i>Sorghastrum nutans</i>	3.4 (2.0)	0.8 (0.7)	5.3 (2.2)	3.1	0.46
<i>Carex</i> spp.	3.4 (1.2)	3.9 (1.0)	1.8 (0.6)	3.1	0.92
<i>Sporobolus</i> spp.	3.3 (1.4)	2.6 (2.6)	2.8 (1.7)	2.9	0.33
<i>Solidago canadensis</i>	3.3 (2.5)	1.8 (0.9)	3.0 (1.9)	2.7	0.33
<i>Schizachyrium scoparium</i>	3.8 (1.7)	1.5 (0.9)	2.5 (1.2)	2.6	0.63
<i>Ratibida pinnata</i>	2.2 (1.2)	2.0 (2.0)	1.9 (1.2)	2.0	0.50
<i>Amorpha canescens</i>	1.5 (1.0)	3.5 (1.6)	0.8 (0.6)	2.0	0.38
<i>Dichanthelium leibergii</i>	1.5 (0.8)	2.5 (1.4)	1.8 (1.4)	1.9	0.50
Standing dead mass	224.2 (32.1)	208.8 (55.0)	313.9 (49.5)		
Litter	255.7 (64.8)	190.2 (29.2)	193.7 (38.3)		

was significantly greater in the cover crop treatment during the 2003 dates (time–contrast interaction; $F_{2,10} = 4.93$, $P = 0.03$; mean richness of 7.3, 11.8 and 14.2 for cover crop and 7.0, 6.9 and 6.5 for no cover crop for September–October 2002, May–June 2003 and August 2003, respectively).

PROPORTION OF β DIVERSITY

After considering accumulated quadrat area, distance was not significantly related to species richness or diversity (richness: mean slope 0.00035, range –0.0097–0.0127, r^2 values ≤ 0.03 ; diversity: mean slope 0.00013, range

Table 2. Results of ANOVA (*F*, *P*-values) for comparisons of community variables (alpha level, 0.4 m²) between a large tallgrass prairie restoration and three remnant prairie sites

Source	d.f.	Proportion exotic biomass*	Proportion exotic S†	Number exotic S‡	Alpha S§	Alpha E¶	Alpha 1/D**
Prairie	3	1.7 (0.19)	10.3 (< 0.01)	4.1 (0.02)	25.1 (< 0.01)	1.3 (0.28)	9.0 (< 0.01)
Restoration vs. remnant site contrast	1	0.02 (0.88)	29.8 (< 0.01)	6.5 (0.02)	60.2 (< 0.01)	0.1 (0.77)	26.3 (< 0.01)
Error	28						
Time	2	8.5 (< 0.01)	0.2 (0.81)	0.7 (0.52)	18.6 (< 0.01)	0.9 (0.40)	10.4 (< 0.01)
Time × prairie	6	1.8 (0.12)	0.6 (0.74)	1.0 (0.42)	1.6 (0.18)	1.3 (0.27)	1.9 (0.10)
Time × restoration vs. remnant site	2	1.7 (0.20)	0.1 (0.88)	1.3 (0.29)	3.4 (0.04)	1.0 (0.38)	1.1 (0.35)
Error (time)	56						

*Biomass of exotic species/total biomass.

†Number of exotic species/total number of species.

‡Number of exotic species.

§Number of species.

¶Simpson's evenness (1/D/S).

**Simpson's diversity (1/D).

Table 3. Above-ground productivity (g m⁻² year⁻¹) (SE) for a large tallgrass prairie restoration (Neal Smith National Wildlife Refuge, NS) and three remnant prairie (A.C. Morris, M; Rolling Thunder, RT; Sheeder, Sh) sites using three methods of estimation

	NS	M	RT	Sh
Peak above-ground biomass 2002 (without consumption)	447 (75)	422 (75)	387 (75)	312 (75)
Peak above-ground biomass 2003 (without consumption)	482 (78)	383 (78)	313 (78)	409 (78)
Peak above-ground biomass 2003 (with consumption)	784 (34)	383 (34)	313 (34)	409 (34)

–0.0001–0.0005, nine *r*² values ≤ 0.04; remaining three between 0.08 and 0.17). Therefore, based on this lack of a relationship, we estimated γ diversity using combined quadrats (Crist *et al.* 2003).

In contrast to our expectations, the proportion of β diversity was 175–226% greater in the restoration sites than in remnant sites (Fig. 4d–f). The proportion of β richness was 104–117% greater in the restoration sites than in remnant sites (Fig. 4a–c).

Discussion

The few studies attempting to determine grassland restoration success have not included restorations that managed both fire and native ungulates, which can affect species richness, evenness and patchiness in intact ecosystems (McNaughton 1979; Hartnett, Hickman & Walter 1996; Collins *et al.* 1998; Knapp *et al.* 1999). Although we found large differences in diversity and NPP between restoration and remnant sites, site managers were able to restore dominant native prairie species and levels of native biomass. The most novel of our findings was that, in contrast to our expectations, we detected a greater proportion of β diversity and richness at the restoration sites, and distance between quadrats did not affect the analysis of spatial diversity components, at least at this scale. The proportion of native biomass may be easier to restore than the very high small-scale species richness and diversity of remnant sites.

Abandoned crop fields often have high levels of nitrogen that can lead to very high productivity in early restoration and conservation plantings (Baer *et al.* 2002; Blumenthal, Jordan & Russelle 2003), and our results were consistent with this trend. Higher NPP might have been at least partially responsible for the lower diversity of the restoration sites if high biomass and litter were suppressing recruitment of rare species.

COVER CROP

Cover crops are thought to influence growth of seedlings positively (Withgott 2000), but few studies have tested this hypothesis. Pywell *et al.* (2002) did not detect a positive influence of a cover crop on diversity, although it significantly reduced the number of unsown grass species after the first year. Our study found that a cover crop significantly increased species diversity, richness and evenness, and reduced the proportion of exotic species. However, treatments were not fully interspersed in the current design and further experimental work is needed to test the generality of these results.

SPECIES DIVERSITY

We found that α diversity and richness were much lower in the restoration than remnant sites. Thus, our results were consistent with other studies examining restoration success that found lower α richness in

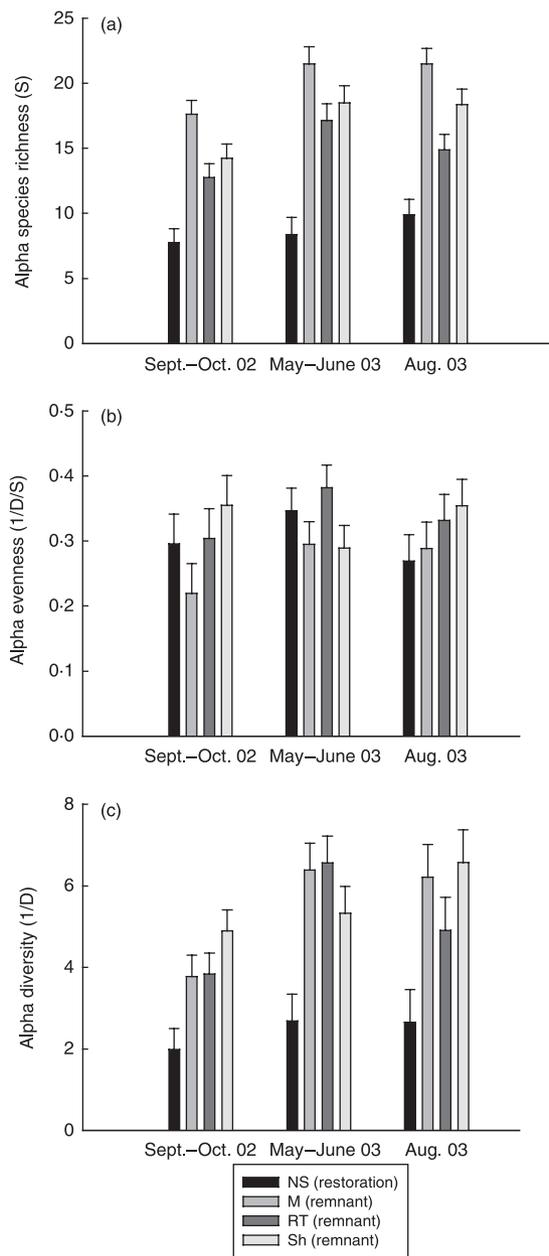


Fig. 3. Alpha (a) species richness, (b) evenness ($1/D/S$) and (c) diversity ($1/D$) for a prairie restoration (Neal Smith National Wildlife Refuge, NS) and three remnant prairie sites. A.C. Morris, M; Rolling Thunder, RT; Sheeder, Sh.

restoration sites (Kindscher & Tieszen 1998; Sluis 2002). Like Polley, Derner & Wilsey (in press), α evenness did not differ between the restoration and remnant sites. Evenness has recently been shown to be affected more by competition than migration processes (B. J. Wilsey & G. Stirling, unpublished data) and our study included grazing in the restoration sites, which has been found to increase evenness in intact systems (McNaughton 1979; Hartnett, Hickman & Walter 1996). Although grazing was not studied directly here, our results suggest that grazing is maintaining high quadrat-scale evenness (where competition among plants takes place) to a level that is comparable with

that of remnant sites. These results imply that small-scale evenness may be easier to restore than richness. Remnant prairies had exceptionally high levels of small-scale species richness (19.0 species 0.4 m⁻² in May–June) and Simpson's diversity (6.1 0.4 m⁻² in May–June) and this may be particularly difficult to restore.

The additive partitioning model provides a useful way of partitioning diversity into spatial components, because diversity at all levels is in the same units (MacArthur, Recher & Cody 1966; Lande 1996), which enables estimation of the proportions of α and β (Veech *et al.* 2002; Crist *et al.* 2003). However, the additive partitioning model could potentially be problematic in cases where sites of different size are randomly sampled and compared. In the original multiplicative partitioning model proposed by Whittaker (1960), β diversity was usually calculated as species turnover with distance along a gradient. The additive partitioning method allows β diversity to be calculated among random samples (Veech *et al.* 2002). Using this method with sites of differing sizes could potentially cause biased estimates of β because of the increased likelihood of encountering different microtopography in large areas (Whittaker 1960; Nekola & White 1999; Balvanera *et al.* 2002; Condit *et al.* 2002). However, we found no relationship with distance at the scale used in our study. This suggests that it might be possible to compare different-sized grasslands with the additive partitioning method.

Allison (2002) described anecdotally that restored prairies have large single-species patches and remnant sites have highly intermingled species, but this has never been quantified until now. High β richness (Wagner, Wildi & Ewald 2000; Crist *et al.* 2003) and β diversity (McNaughton 1983; Harrison & Inouye 2002) have been found in many systems and taxa. Although there was high dominance and few species per quadrat in the restoration sites, the proportions of β diversity and richness were greater than in remnant sites because the identity of the dominant species changed between quadrats in the restoration sites. Combining quadrats decreased the relative abundance of each dominant species and increased the number of species, thereby increasing evenness and richness and thus overall diversity. Remnant sites, however, were particularly species rich (Monsen 2001) and had very high evenness, even at the quadrat level, so combining quadrats did not increase diversity as much. One possible explanation for the greater proportion of β diversity in the restoration sites is that dominant species might spread from a local point to form a larger, more clumped distribution during early years of establishment (Sluis 2002; Derner *et al.* 2004). A prediction stemming from this hypothesis is that species patches should be larger in restoration than in remnant sites (Derner *et al.* 2004).

Although positive effects of native ungulates on diversity and spatial variability are well-documented in intact grasslands (Hartnett, Hickman & Walter 1996; Collins *et al.* 1998; Knapp *et al.* 1999), their effects on restoration sites have not been reported. Our findings

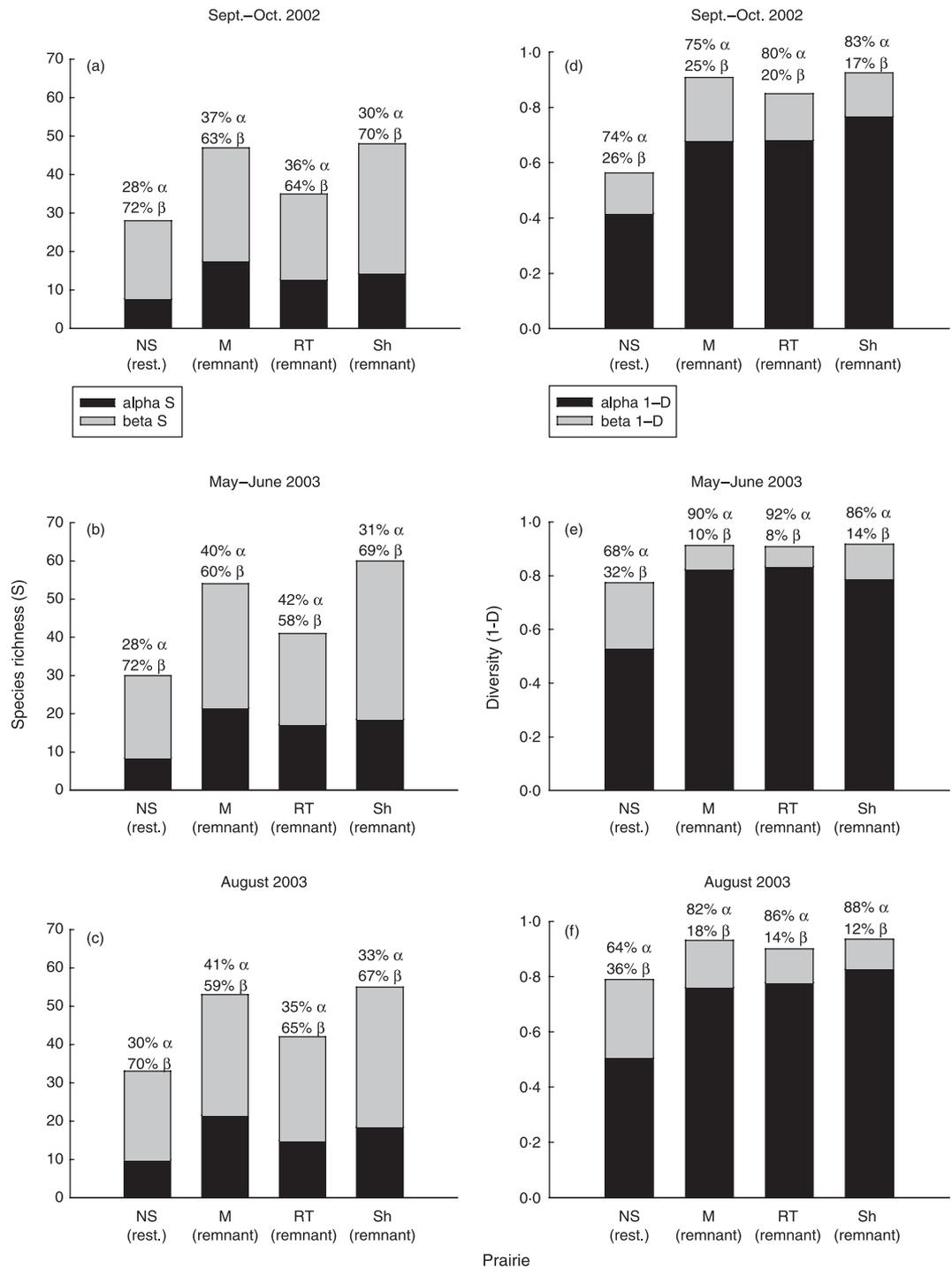


Fig. 4. Alpha and beta (a–c) richness and (d–f) diversity (1 – D) using the additive partitioning method for a prairie restoration (Neal Smith National Wildlife Refuge, NS) and three remnant (A.C. Morris, M; Rolling Thunder, RT; Sheeder, Sh) sites. Gamma values are represented by the top line of each bar. The proportions of γ that are α and β are given by percentages above each bar.

suggest that positive effects of native ungulates may be negated in restoration sites if rare species are unable to colonize disturbance sites, because species pools may regulate richness in some situations (Gough, Grace & Taylor 1994; Pywell *et al.* 2002; Foster & Tilman 2003). Alternative hypotheses for low richness in restorations include: (i) frequent spring burning of restorations, which may promote increased production of dominant C_4 grasses (Howe 2000), which may in turn suppress

establishment of other species; and (ii) at 8–10 years old, restoration sites may not be old enough to have developed the high diversity of remnant sites.

Finally, we found that even a very large restoration project was unable to restore fully all aspects of species diversity. Surprisingly, neighbourhood-scale species diversity appeared to be the hardest to restore. To restore fully the spatial patterns in species richness and diversity, grassland restoration sites should be managed

for high levels of species co-existence at the neighbourhood scale, which characterizes remnant sites. Therefore, management regimes should focus on local-scale restoration methodologies such as mowing (Holl & Crone 2004). Keeping plants small and dense during the earliest stages of development could help in restoring high small-scale species diversity.

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