



Shifting dominance from native C₄ to non-native C₃ grasses: relationships to community diversity

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Many field studies have examined how site fertility, soil differences and site history influence the diversity of a plant community. However, only a few studies have examined how the identity of the dominant species influences the diversity in grasslands. Plant species differ widely in phenology, growth form and resource uses; thus, communities dominated by different species are also likely to strongly differ in the environment that they create and in which the subdominant species exist. We examined the correlation between the four most dominant species and community diversity in 2100 plots, located in 21 abandoned agricultural fields in central Minnesota over a 23-year period. The four most common species were two non-native C₃ cool season species, *Poa pratensis* and *Agropyron repens*, and two native C₄ warm season species, *Schizachyrium scoparium* and *Andropogon gerardii*. We found that the differences in the dominants explained up to 27% of the community diversity. Thus, the identity of the dominant species can have a strong influence on community diversity and studies examining factors that influence plant community diversity need to incorporate the effect of the dominants. Secondly, we found that the non-native C₃ grass dominated communities had lower overall and lower native species richness relative to the native C₄ grass dominated communities. Therefore, a shift in dominants from C₄ to C₃ may lead to a large community diversity decline. We found that *Poa pratensis*, the most abundant non-native C₃ grass increased in abundance over the 23 years; thus, the negative influence of non-natives on the community diversity is not decreasing over time and active management is required to restore native grassland plant communities.

Plant community diversity is controlled by a combination of factors, such as nutrient availability (Tilman and Olff 1991, Vitousek et al. 1997), grazing and fire regimes (Knops 2006, Dorrrough et al. 2007), and recruitment limitation (Foster and Tilman 2003, MacDougall and Turkington 2006, Zeiter et al. 2006). In addition to these factors, several studies have examined how non-native species abundance correlates with community diversity (Wilson and Belcher 1989, Meiners et al. 2002, Chornesky and Randall 2003) and how native and non-native abundance/richness correlates within grassland systems (Cleland et al. 2004, Davies et al. 2005, Maskell et al. 2006b).

Grassland plant communities are dominated by one to three grass species (Freeman 1998), commonly referred to as 'matrix species' (Grubb 1986, Collins 1991, Hartnett and Fay 1998), which often account for more than 40% of the total plant cover. The dominant matrix species influences the environment and the available niches in which the sub-dominant community exist (Emery and Gross 2007). However, the sub-dominant plant community contributes the majority of the plant diversity found in these systems (Hartnett and Fay 1998, Cully et al. 2003, Smith and Knapp 2003). The sub-dominant plant community is composed of an array of forb, grass, and woody

species and each individual sub-dominant species typically accounts for less than five percent of the total plant cover (Grubb 1986, Collins and Glenn 1991).

Many studies have examined drivers that influence community diversity, such as dispersal ability (Foster and Tilman 2003, Gross et al. 2005), field age (Inouye et al. 1987), field disturbance history (Gross et al. 2005), soil fertility (Gross et al. 2005) and productivity. However, the identity of the dominant species on sub-dominant diversity has been relatively unexplored (Wilson and Belcher 1989, Christian and Wilson 1999, Henderson and Naeth 2005, Emery and Gross 2006). In addition, the association of the dominant species identity with the proportion of native versus non-native richness within the sub-dominant plant community is also relatively unexplored (Crall et al. 2006).

Matrix species in the tallgrass prairies of the central Great Plains are typically native C₄ warm season bunchgrasses, such as *Andropogon gerardii*, *Schizachyrium scoparium*, *Panicum virgatum* and *Sorghastrum nutans* (Freeman 1998, Hartnett and Fay 1998, Cully et al. 2003). However, in many grassland systems, both successional and undisturbed, non-native C₃ cool season sod-forming grasses, such as *Poa pratensis*, *P. compressa* and *Bromus inermis*, are increasing in abundance, and in some areas are replacing the native matrix species (Tyser

1992, Chapin et al. 2000, Chornesky and Randall 2003). There are several key differences between the native and the non-native matrix grasses. First, the native matrix grasses utilize the C₄ photosynthetic pathway, while the non-native matrix grasses utilize the C₃ pathway. The C₄ photosynthetic pathway causes higher nitrogen and water use efficiency relative to the C₃ photosynthetic pathway (Wedin 2004), which leads to higher biomass production resulting in lower light availability and often lower soil nitrogen and water levels. Secondly, the non-native C₃ matrix species tend to be sod-forming grasses (McGregor et al. 1991) which provide less space to the sub-dominant species compared to the bunch growth form of the native C₄ matrix grass species (McGregor et al. 1991). Thirdly, there are differences in phenology between the native and non-native matrix species. The native matrix grasses are warm season species, active during the peak of the summer season, with the majority of their growth occurring between mid-June and late-August. The non-native matrix grasses are cool season species, active during the cooler parts of the season, with their peak growth occurring during late spring/early summer and late summer/early fall (Kemp and Williams III 1980).

A large proportion of the sub-dominant plant community in grasslands of the central Great Plains consists of other C₃ cool season species that overlap in their active growing season with the non-native matrix grasses. Previous studies suggest that competition is stronger between native resident species and invaders with similar requirements (Christian and Wilson 1999, Fargione and Tilman 2005a, 2005b). Therefore, the overlap in growing season and water and resource requirements could result in increased competition between the non-native matrix grasses and the sub-dominant species. As a result of increased competition, dominance by the non-native matrix species could potentially lower overall community diversity compared with communities dominated by the native matrix species, which are phenologically asynchronous with a large proportion of the sub-dominant species. Furthermore, the differences in phenology, resource use and growth form between the native and non-native matrix species cause the niches and spaces available to the sub-dominant plant species to vary between these communities. The native sub-dominant species have adapted to existence within a native matrix over evolutionary time, whereas the non-native sub-dominant species might be better adapted to existence within a non-native matrix, a trend that has been seen in previous studies (Crall et al. 2006, Maskell et al. 2006a, 2006b).

We used data from a long-term study of an abandoned field chronosequence at Cedar Creek Natural History Area in central Minnesota to examine how the identity of the matrix species, specifically native C₄ grasses versus non-native C₃ grasses, correlates with plant diversity in tallgrass prairies. These fields are dominated by a mixture of native (*Andropogon gerardii* and *Schizachyrium scoparium*) and non-native (*Poa pratensis* and *Agropyron repens*) grasses, and this diverse plant community allowed us to explore if and how community diversity corresponds to the identity of the matrix species. We explored correlational patterns between the identity of the matrix grasses and several diversity parameters, including total species richness, Shannon evenness index, Shannon diversity index, native species

richness, and non-native species richness. These correlational patterns helped us address two main hypotheses:

1. Dominance by non-native C₃ cool season grasses is associated with lower community diversity (estimated by the parameters species richness, evenness, and diversity) relative to dominance by native C₄ warm season grasses. The rationale for this hypothesis is that the non-native matrix species and the native matrix species will differ in their interactions with the sub-dominant community due to the differences in their phenology, resource use, and growth form.
2. Dominance by non-native C₃ cool season grasses is associated with lower native species richness and higher non-native species richness relative to dominance by native C₄ warm season grasses. This hypothesis is based on previous studies which have found native dominated communities to be comprised of more native species, while non-native dominated communities tend to have a higher proportion of non-native species (Crall et al. 2006, Kulmatiski 2006, Maskell et al. 2006b).

Material and methods

Site

This study was conducted within 21 abandoned agricultural fields (hereafter referred to as old fields) at the Cedar Creek Natural History Area (Cedar Creek) in south central Minnesota. Cedar Creek is a 2200 ha reserve, and the landscape is a mosaic of tallgrass prairie, open oak savanna, mixed deciduous-boreal forest and wetlands. Many of the prairies and oak savannas were previously cultivated and were abandoned 10 to 79 years ago (Inouye et al. 1987). Cedar Creek is located on a sandy glacial outwash, and soils are composed of 1–5% silt, 1–4% clay, and 92–97% sand. The soil is low in organic matter, nitrogen, and has poor water holding capacity (Grigal et al. 1974). The climate of Cedar Creek is characterized by cold winters and hot humid summers, with summer temperature averaging around 14°C. The last spring freeze falls around 9 May, and the first fall freeze is around 27 September. Average annual rainfall at Cedar Creek is 775 mm (1950–1993), with 72% of the precipitation occurring between May–October (Knops and Tilman 2000).

The old fields range in age since abandonment from 10 to 79 years and, prior to abandonment, were cultivated with potatoes, maize, oats, soybeans or rye. All fields are located on well-drained nitrogen poor sandy soils with slopes ranging between 0–15% (Inouye et al. 1987). For this long term study, nineteen fields ranging in successional age were selected in 1983 throughout Cedar Creek, one field was added in 1993, and another field was added 2000, resulting in 19 fields for the 1983 and 1989 surveys, 20 fields for the 1994 and 1997 surveys, and 21 fields for the 2002 and 2006 surveys. Each field contains 4 permanent 40 m transects that are spaced 25 m apart. Along each transect there are 25 permanent 1.0 × 0.5 m plots spaced 1.5 m apart, accounting for a total of 100 plots per field.

Plant abundances and diversity parameters

Plant abundances were estimated for the 0.5 m² plots six times over a 23-year period; in 1983, 1989, 1994, 1997, 2002 and 2006. All sampling was conducted in mid July of each year over a two-week period; this captures the late part of the phenology for the cool season species and the early part of the phenology for the warm season species. Voucher specimen of all species are archived at Cedar Creek and were used standardize species over the different sampling years. Each field consisted of four transects of 25 plots each. Four pairs of two people estimated cover with each pair estimating one transect in each field. The people collecting the cover data calibrated species identification and cover estimates with the archived voucher specimen and with each other prior to and during the data collection.

Plants were identified to species, and the exact percent cover of each species, bare ground, plant litter, moss and lichens were determined. Total cover was constrained to 100%. There were a few instances where seedlings could not be identified to the genus or species level. The seedlings identifiable to only the genus level were labeled as the genus sp. The seedlings unidentifiable to the genus level were grouped into a miscellaneous category: miscellaneous forbs, miscellaneous grass, miscellaneous legume, and miscellaneous woody. Only 2.04% of all plots in all sampling years contained species in the miscellaneous categories, and miscellaneous cover averaged only 0.08% of relative cover across all sampling years.

Using the cover data, we calculated total vascular plant cover, relative percent cover of each species as percent of total vascular plant cover, species richness, Shannon species evenness, and Shannon community diversity (Zar 1984). Species richness was then divided into native species richness and non-native species richness. Species were designated as either native or non-native using Flora of the Great Plains (1986) as a reference guide (Supplementary material Appendix 1). These parameters were estimated for each sampling year. Species richness is the total number of species present within the plot. Species evenness calculates

how evenly total plant cover is divided amongst all species present within the plot (Eq. 1). This value can range between zero and one, with zero indicating a highly uneven community and one indicating a community with all present species having equal abundance (Zar 1984). Community diversity combines both species richness and species evenness into one quantitative value (Eq. 2), with higher values indicating more diverse communities. Both species evenness (J) and community diversity (H) were calculated using the Shannon index (Eq. 1, 2) (Zar 1984).

$$J = H/\ln(S) \quad (1)$$

$$H = \sum (P_i \times \ln(P_i)) \quad (2)$$

Where S is the species richness of the plot and P_i is the relative percent cover of the ith species in the plot.

Matrix species

The old fields of Cedar Creek are dominated by grasses, such as *Schizachyrium scoparium* (little blue stem) and *Andropogon gerardii* (big blue stem) (both native C₄ warm season bunch grasses), and *Poa pratensis* (Kentucky blue grass) and *Agropyron repens* (quackgrass) (both non-native (Eurasian) C₃ cool season, sod forming grasses). These four species were selected for this study because of their commonness and high abundance in the old fields, contributing 46 to 64% of the total vascular plant cover (Table 1). *Poa pratensis* is the most abundant species present in the old fields of Cedar Creek, with its abundance more than twice the abundance of all other species (Table 1) and *P. pratensis* is also present in the highest percentage of total plots, making it the most common species to occur at Cedar Creek. This is a striking contrast to the prevalence of the native matrix-forming grass species, *A. gerardii* and *S. scoparium*, which were found in less than 40% of all plots in each sampling year. Despite their rarity as dominants relative to *P. pratensis*, both native grass species have comparable mean relative abundance, showing that the

Table 1. Mean values plus one standard error of the mean are given for the relative percent cover of the 10 most abundant species in the Cedar Creek old fields and for the estimated diversity parameter including total vascular plant cover, species richness, Shannon evenness (J), Shannon diversity (H), native species richness and relative percent cover, and non-native species richness and relative percent cover in each sampling year.

	1983	1989	1994	1997	2002	2006
<i>Poa pratensis</i>	^a 23.58 ± 0.60	^b 20.76 ± 0.60	^c 31.04 ± 0.65	^d 33.11 ± 0.65	^e 26.91 ± 0.55	^c 30.48 ± 0.60
<i>Schizachyrium scoparium</i>	^a 4.81 ± 0.33	^b 10.47 ± 0.55	^{bc} 10.31 ± 0.46	^d 12.80 ± 0.53	^b 10.70 ± 0.45	^c 9.15 ± 0.41
<i>Agropyron repens</i>	^a 10.39 ± 0.45	^b 8.81 ± 0.32	^a 9.92 ± 0.40	^c 11.91 ± 0.43	^{bd} 7.79 ± 0.35	^d 7.73 ± 0.28
<i>Andropogon gerardii</i>	^a 6.96 ± 0.44	^b 7.06 ± 0.45	^a 6.83 ± 0.42	^a 5.97 ± 0.36	^a 5.98 ± 0.36	^b 8.47 ± 0.45
<i>Vicia villosa</i>	^{ab} 1.27 ± 0.13	^c 2.91 ± 0.22	^a 0.58 ± 0.05	^b 1.72 ± 0.13	^d 9.13 ± 0.41	^e 7.80 ± 0.38
Carex sp.	^a 1.59 ± 0.14	^b 3.45 ± 0.23	^c 7.43 ± 0.34	^c 8.19 ± 0.32	^c 7.87 ± 0.32	^d 5.80 ± 0.29
<i>Rumex acetosella</i>	^a 3.15 ± 0.18	^a 3.39 ± 0.23	^b 4.02 ± 0.20	^c 2.27 ± 0.14	^d 5.47 ± 0.26	^a 3.29 ± 0.20
<i>Solidago gigantea</i>	^a 1.94 ± 0.21	^a 2.10 ± 0.23	^b 1.01 ± 0.13	^b 1.39 ± 0.14	^b 1.35 ± 0.12	^a 2.01 ± 0.19
<i>Bromus inermis</i>	^a 0.11 ± 0.05	^a 0.25 ± 0.07	^a 0.32 ± 0.06	^b 0.77 ± 0.12	^b 1.04 ± 0.14	^c 1.60 ± 0.18
<i>Crepis tectorum</i>	^a 4.37 ± 0.28	^b 0.24 ± 0.04	^c 1.22 ± 0.09	^d 0.71 ± 0.08	^c 1.45 ± 0.12	^c 1.53 ± 0.16
Plant cover	^a 44.62 ± 0.38	^b 24.55 ± 0.31	^a 44.04 ± 0.36	^c 51.27 ± 0.29	^d 34.46 ± 0.31	^e 22.89 ± 0.32
Total richness	^a 8.25 ± 0.07	^b 6.55 ± 0.05	^c 7.25 ± 0.06	^b 5.95 ± 0.06	^b 6.60 ± 0.05	^d 6.00 ± 0.05
Evenness (J)	^a 0.67 ± 0.00	^b 0.68 ± 0.00	^c 0.64 ± 0.00	^{ab} 0.67 ± 0.00	^{ad} 0.67 ± 0.00	^d 0.65 ± 0.00
Diversity (H)	^a 1.38 ± 0.01	^b 1.26 ± 0.01	^{bc} 1.24 ± 0.01	^d 1.17 ± 0.01	^c 1.22 ± 0.01	^e 1.14 ± 0.01
Native richness	^a 5.29 ± 0.07	^b 4.00 ± 0.05	^c 4.51 ± 0.06	^d 3.37 ± 0.06	^e 3.77 ± 0.05	^d 3.44 ± 0.06
Non-native richness	^a 2.95 ± 0.03	^b 2.55 ± 0.03	^c 2.73 ± 0.03	^b 2.57 ± 0.03	^d 2.83 ± 0.03	^b 2.59 ± 0.03
Native % relative cover	^a 52.06 ± 0.74	^b 56.38 ± 0.80	^c 48.60 ± 0.76	^d 45.99 ± 0.79	^d 45.96 ± 0.73	^d 45.92 ± 0.80
Non-native % relative cover	^a 47.92 ± 0.74	^b 43.62 ± 0.80	^c 51.34 ± 0.76	^d 53.99 ± 0.79	^d 54.10 ± 0.73	^d 54.20 ± 0.79

native matrix species are able to attain degrees of dominance equal to that of *P. pratensis*. *Schizachyrium scoparium* was the second most abundant species in all sampling years except for 1983, and *A. repens* and *A. gerardii*, were the third and fourth most abundant species in most sampling years (Table 1).

The purpose of this study is to compare mean diversity parameter estimates in plots dominated by native C₄ matrix grass species (*A. gerardii* and *S. scoparium*) versus plots dominated by non-native C₃ matrix grass species (*P. pratensis* and *A. repens*). Therefore, for the purpose of this study we only used the plots in which one of the four matrix species of interest are dominant. Dominance is defined as comprising 40% or more of the relative plant cover. The number of plots dominated by each of the matrix species varied from year to year, but the average number of plots, across sampling years, in which each matrix species was dominant corresponded with how they ranked in abundance across sampling years (Table 1); N_{ave} (*P. pratensis*) = 599, N_{ave} (*S. scoparium*) = 230, N_{ave} (*A. gerardii*) = 170, N_{ave} (*A. repens*) = 119.

Analyses

Our first hypothesis predicted that dominance by non-native C₃ matrix species is associated with lower diversity, as estimated by species richness, Shannon evenness and Shannon diversity, compared to dominance by native C₄ matrix species. We tested this hypothesis using a MANOVA with species richness, Shannon evenness and Shannon diversity as the dependent factors and the model included sampling year, photosynthetic pathway (native C₄ versus non-native C₃), and the interaction between sampling year and photosynthetic pathway. For this analysis, field age was included as a covariate. When the MANOVA was significant, we examined species richness, Shannon evenness and Shannon diversity separately to determine which of these factors was driving the overall significance. In addition, if sampling year was significant, we then conducted an ANOVA for each sampling year to determine if the patterns associated with photosynthetic pathway were consistent across sampling years or if they varied (i.e. higher species richness associated with dominance by C₄ species in each sampling year). Some of dataset had a distribution significantly different from normal, however, transformations showed the same significances and only minor changes in F and R² values.

Our second hypothesis predicted that dominance by non-native C₃ matrix species is associated with lower native species richness and higher non-native species richness compared to dominance by native C₄ matrix species. We tested this hypothesis following the same methods used to test our first hypothesis except with native species richness and non-native species richness as the dependent factors in the model.

All analyses were performed using SPSS ver. 15.0.

Results

Plant abundances and diversity parameters

Vascular plant cover varied from 23% to 51% depending on the sampling year; consequently, we calculated all vegetation parameters as relative percent cover of total vascular plant cover (Table 1). In total, these abandoned agricultural fields had 43–54% relative cover by non-native plant species. Six of the ten most abundant species were non-native, including two of the four most abundant grass species (Table 1). The overall species richness ranged from 6.0 to 8.3 species per 0.5 m⁻² and non-native species comprised 36–43% of the total species present, depending on sampling year. Of the 256 plant species present across all plots in all years, 213 (83%) were native species and 43 (17%) were non-native species (Supplementary material Appendix 1).

Hypothesis one

Species richness, Shannon evenness and Shannon diversity

The MANOVA showed a significant effect of photosynthetic pathway (C₃ vs C₄ species), sampling year, and the interaction of photosynthetic pathway and sampling year on overall diversity estimated by species richness, Shannon evenness and Shannon diversity (Table 2). When each of the diversity parameters were examined separately there was a significant effect of photosynthetic pathway, sampling year, and the interaction of photosynthetic pathway and sampling year on species richness, Shannon evenness and Shannon diversity (Table 2). Consistent with our hypothesis, dominance by the non-native C₃ matrix species was associated with significantly lower species richness in all sampling years (Fig. 1A, a). However, although there was a significant effect of photosynthetic pathway on Shannon evenness, there were no consistent trends across sampling

Table 2. Community diversity: multivariate analysis of total species richness, Shannon evenness and Shannon diversity by photosynthetic pathway (dominance by C₃ vs C₄ matrix species), sampling year, and photosynthetic pathway × sampling year, with field age and % *Poa pratensis* cover as a co-variables. F-values are given (MANOVA F-values are of the Pillai's trace). ***p < 0.0001. ns=not significant.

Factor	(DF)	Overalls MANOVA	Total species richness	Shannon evenness (J)	Shannon diversity (H)
Corrected model	(13, 8284)		161.3*** R ² = 0.202	82.6*** R ² = 0.115	180.0*** R ² = 0.221
Photosynthetic pathway: C ₃ versus C ₄	(1, 8284)	113.7***	227.5***	68.2***	35.4***
Sampling year	(5, 8284)	40.1***	111.5***	12.6***	26.2***
Photosynthetic pathway × sampling year	(5, 8284)	13.7***	12.1***	25.0***	25.3***
Co-variable % <i>Poa pratensis</i>	(1, 8284)	139.2***	122.6***	285.2***	402.1***
Co-variable: field age	(1, 8284)	156.9***	0.0 ^{ns}	470.2***	220.9***

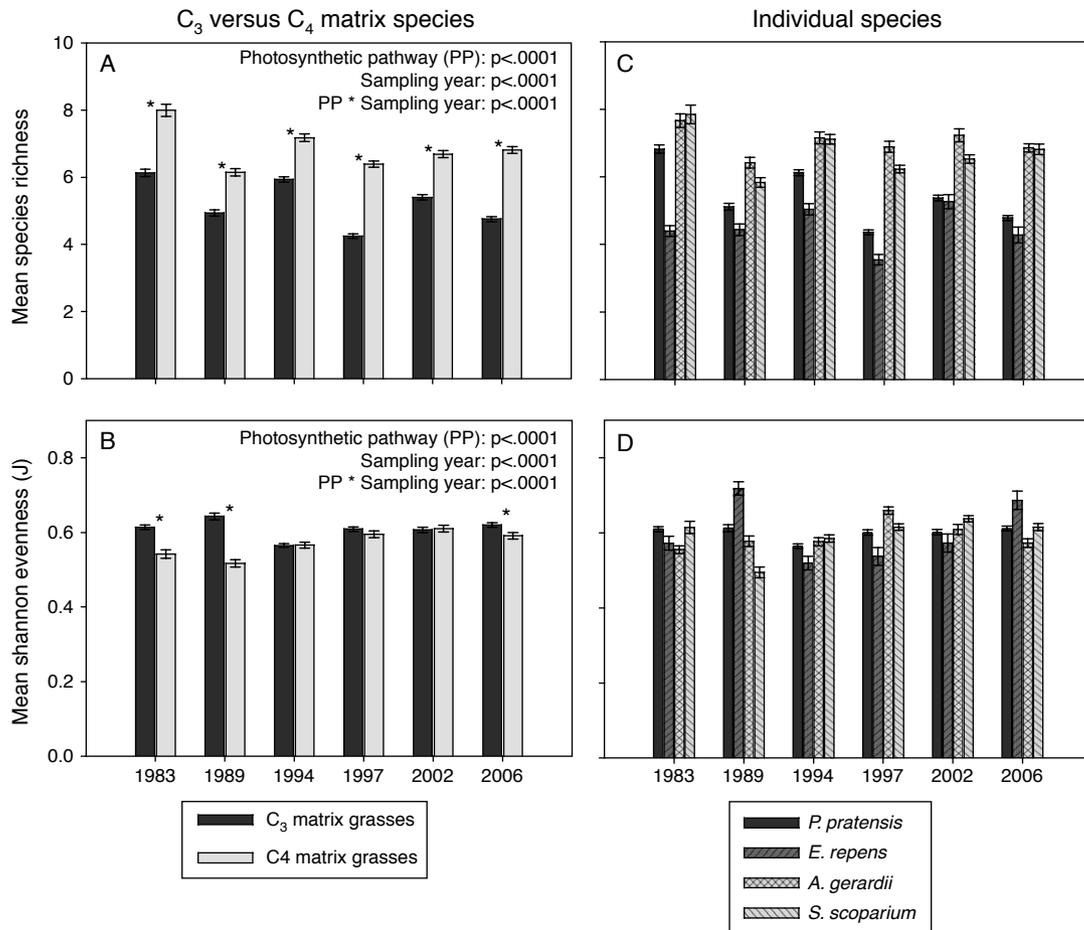


Figure 1. Species richness (A, a) and Shannon evenness (B, b) of plots where different matrix grasses are dominant (i.e. comprise 40% or more of the relative total plant cover). Left column (denoted by capital letters) shows comparison of mean parameter estimates between photosynthetic pathways (PP); plots dominated by non-native C₃ matrix species (dark gray bars) and plots dominated by native C₄ matrix species (light gray bars). Right column (denoted by lower-case letters) shows a comparison of the mean parameter estimates between plots dominated by the four different matrix species examined. All error bars represent one standard error above and below the mean and asterisks signify significant differences between plots dominated by native C₄ species and non-native C₃ species (p < 0.05). N_{ave} (*P. pratensis*) = 599, N_{ave} (*E. repens*) = 119, N_{ave} (*A. gerardii*) = 170, N_{ave} (*S. scoparium*) = 230.

years between the non-native C₃ matrix species and the native C₄ matrix species (Fig. 1B, b). The patterns between the C₃ versus the C₄ matrix species in regards to Shannon diversity mimicked the patterns seen with species richness. Since the Shannon diversity parameter is strongly influenced by species richness (Smith and Wilson 1996), we will not discuss this parameter in efforts to avoid redundancy.

Hypothesis two

Native and non-native species richness

The MANOVA showed a significant effect of photosynthetic pathway, sampling year, and the interaction between photosynthetic pathway and sampling year on native and non-native species richness (Table 3). When these parameters were examined separately there was a significant

Table 3. Native and non-native species richness: multivariate analysis of native species richness and non-native species richness by photosynthetic pathway (dominance by C₃ vs C₄ matrix species), sampling year, and photosynthetic pathway × sampling year, with field age and % *Poa pratensis* cover as a co-variables. F-values are given (MANOVA F-values are of the Pillai's trace). ***p < 0.0001.

Factor	(DF)	Overall MANOVA	Native richness	Non-native richness
Corrected model	(13, 7023)		214.7*** R ² = 0.284	52.2*** R ² = 0.088
Photosynthetic pathway: C ₃ versus C ₄	(1, 7023)	593.180***	120.8***	176.4***
Sampling year	(5, 7023)	51.379***	111.7***	28.6***
Photosynthetic pathway × sampling year	(5, 7023)	18.6***	12.0***	25.3***
Co-variable: % <i>Poa pratensis</i>	(1, 7023)	393.3***	434.8***	351.8***
Co-variable: field age	(1, 7023)	128.4***	59.6***	197.2***

effect of photosynthetic pathway, sampling year and the interaction between photosynthetic pathway and sampling year on both native species richness and non-native species richness (Table 3). Consistent with our hypothesis, dominance by the non-native C_3 matrix species was associated with significantly lower native species richness (Fig. 2A, a) in all sampling years. However, the results of our analyses rejected our hypothesis that dominance by the non-native C_3 matrix species corresponded with higher non-native species richness relative to dominance by the native C_4 matrix species. Although there was a significant effect of photosynthetic pathway on non-native species richness, there were no consistent trends across sampling years between the non-native C_3 matrix species and the native C_4 matrix species across sampling years (Fig. 2B, b).

When we examined the non-native species richness associated with dominance by each of the matrix species examined, we observed that in the last four sampling years dominance by the native C_4 matrix species, *S. scoparium*, was associated with non-native species richness equal

to or greater than that associated with dominant by the non-native C_3 matrix species, *P. pratensis* (Fig. 2B). Examining this result, we compared the average relative cover of non-native species associated with dominance by each matrix species (Fig. 3). (For this analysis the cover of *P. pratensis* and *A. repens* were excluded from the tally of non-native cover in the plots where they were dominant, respectively). Again, we observed that in the last four sampling years, dominance by *S. scoparium* was associated with mean relative cover of non-native species equal to or greater than the mean relative cover of non-native species associated with dominance by *P. pratensis* (Fig. 3). However, in the plots where *S. scoparium* was dominant, *P. pratensis* comprised 50% or more of the mean non-native cover (Fig. 4) and in the plots dominated by *A. gerardii*, *P. pratensis* comprised almost 75% or more of the mean non-native cover (Fig. 4). In other words, *P. pratensis* had a substantial presence in the plots dominated by *S. scoparium* and *A. gerardii* and this presence might have influenced the diversity patterns observed. In addition, this result revealed

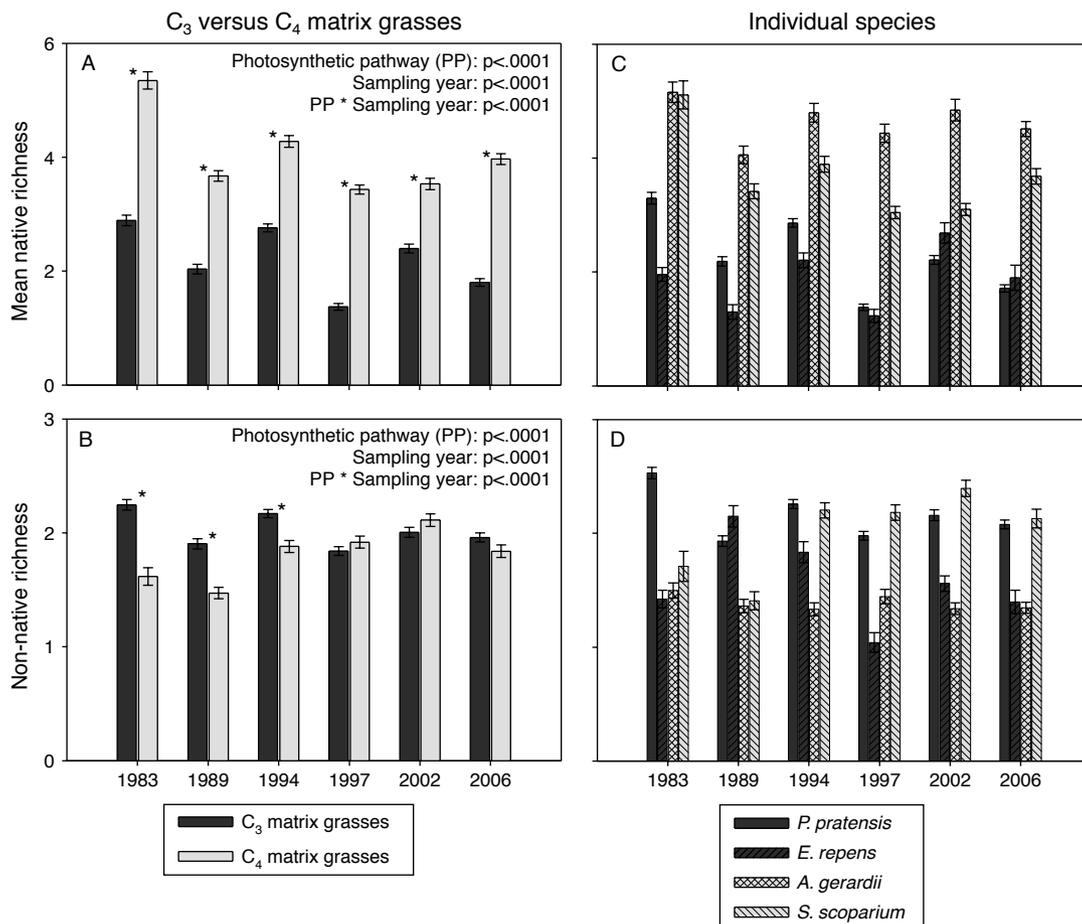


Figure 2. Native species richness (A, a) and non-native species richness (B, b) of plots dominated by different matrix grasses (i.e. comprise 40% or more of the relative cover). Left column (denoted by capital letters) shows comparison of mean native and non-native species richness between photosynthetic pathways (PP); plots dominated by non-native C_3 matrix species (black bars) versus plots dominated by native C_4 matrix species (gray bars). Right column (denoted by lower-case letters) shows a comparison of the mean native and non-native species richness between plots dominated by the four different matrix species examined. All error bars represent one standard error above and below the mean and asterisks signify significant differences between plots dominated by native C_4 species and non-native C_3 species ($p < 0.05$). N_{ave} (*P. pratensis*) = 599, N_{ave} (*E. repens*) = 119, N_{ave} (*A. gerardii*) = 170, N_{ave} (*S. scoparium*) = 230.

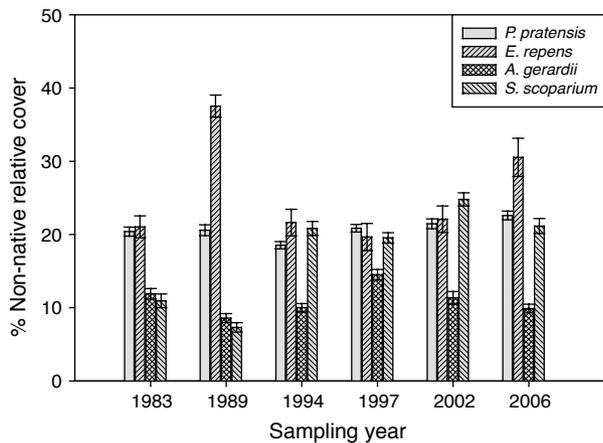


Figure 3. Mean relative percent cover of non-native species in plots dominated by different matrix species (i.e. comprise 40% or more of the relative total plant cover). N_{ave} (*P. pratensis*) = 599, N_{ave} (*E. repens*) = 119, N_{ave} (*A. gerardii*) = 170, N_{ave} (*S. scoparium*) = 230.

that, excluding *P. pratensis*, the non-native species in native dominated plots were, in fact, the rare species found in very low abundances compared to the relative cover of non-native species in plots dominated by *P. pratensis*.

Discussion

We hypothesized that dominance by non-native C_3 matrix-forming grass species would be associated with lower diversity (estimated by species richness and Shannon evenness index) relative to dominance by native C_4 matrix-forming grass species. The results of this study supported our first hypothesis with respect to species richness, but there were no discernable trends in regards to Shannon evenness between the native and non-native

matrix species. Our second hypothesis, which predicted that dominance by non-native C_3 matrix-forming grass species would be associated with lower native species richness and higher non-native species richness compared to dominance by native C_4 matrix-forming grass species, was supported in regards to native species richness, but not in regards to non-native richness.

Species richness was significantly higher in plots dominated by the native matrix species compared to plots dominated by non-native matrix species. These results agree with a study by Wilson and Belcher (1989), which found species richness of native prairie communities to be twice as high as the species richness in communities dominated by non-native species. Similarly, Christian and Wilson (1999) compared old fields with different dominant species in southern Canadian grasslands and found lower species richness in old fields dominated by the non-native C_3 grass *Agropyron cristatum* as compared to old fields dominated by the native C_4 grass *Bouteloua gracilis*.

There was no striking difference in Shannon evenness between communities with different matrix species, especially when comparing dominance by the native C_4 versus non-native C_3 matrix species. This result is likely a function of how Shannon evenness is calculated. Shannon evenness estimates how equally abundant the present species are relative to each other. For example, a community with five species all comprising 20% of the vegetation would be a highly even community. As one of the species becomes more abundant, the other species inherently become less abundant (relatively), and the evenness of the community decreases. Despite the lower occurrence of the native matrix species, *A. gerardii* and *S. scoparium*, compared to *P. pratensis*, we found that when the native matrix species were dominant, they attained relative abundances equal to that of the non-native matrix species when they were dominant. Therefore, we are already considering reduced community evenness due to the presence of a highly dominant species. The only sampling year that a distinct trend in evenness was seen was in 1989, where dominance

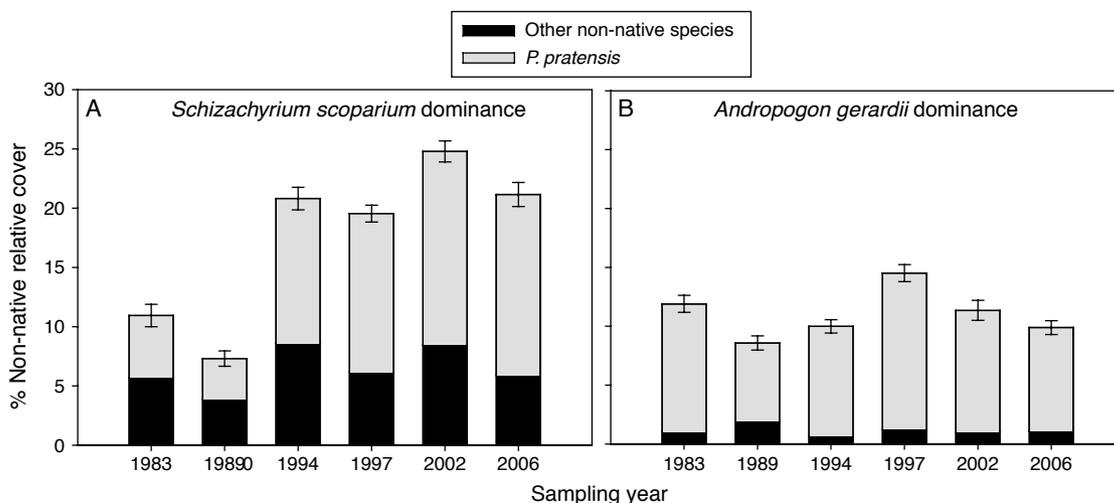


Figure 4. Non-native relative cover of plots dominated by (i.e. comprise 40% or more of the relative total plant cover) native matrix species, *S. scoparium* (A) and *A. gerardii* (B). Non-native relative cover is broken down into relative cover of *P. pratensis* (gray portion of vertical bars) and relative cover of all other non-native species (black portion of vertical bars). N_{ave} (*A. gerardii*) = 170, N_{ave} (*S. scoparium*) = 230.

by the native matrix species corresponded with lower community evenness relative to dominance by the non-native matrix species (Fig. 1b). The drought conditions of that sampling year, and the couple years previous, provide a strong possible explanation for this result. The mean cumulative rainfall (mm) for 1987/1988 was 45% below the mean cumulative rainfall for Cedar Creek during the period between 1982 to 1990 (Tilman and El Haddi 1992). The native C_4 matrix grasses are drought tolerant (Wedin 2004), especially in comparison with the non-native C_3 matrix grasses. During the drought years, the native matrix grass species were released from inter-specific competition with the less drought tolerant species and able to increase in abundance, thereby decreasing community evenness where they were present.

The results of our study supported our second hypothesis in regards to native species richness, but not in regards to non-native species richness. Native species richness was consistently and significantly higher in plots dominated by the native C_4 matrix species compared to plots dominated by non-native C_3 matrix species. These results are similar to findings in a study by Cleland et al. (2004) which found a corresponding decline in native species richness with increasing non-native abundance. Niche complementarity is a strongly supported explanation for these observed trends (Christian and Wilson 1999, Craine et al. 2002, Fargione and Tilman 2005b, Kahmen et al. 2006). Christianson and Wilson (1999) found, in regards to composition, *A. cristatum* tended to exclude species that were more similar in morphological and phenologically characteristics. In addition, Fargione and Tilman (2005b) found, due to phenological and rooting depth differences, an increased abundance of *S. scoparium* was highly correlated with a decline in proportional cover and richness of species with similar phenological and morphological characteristics and an increase in proportional cover and richness of dissimilar species. These examples of niche complementarity go along with our theoretical framework that shifting dominance from native C_4 to non-native C_3 species alters the niches available to the sub-dominant community in terms of phenological and resource use patterns.

Dominance by the native matrix species, *A. gerardii*, was associated with significantly lower non-native species richness compared to dominance by the non-native matrix species, *P. pratensis* (Fig. 2b). However, since there were no consistent trends seen with the other non-native matrix species, *A. repens*, nor the other native matrix species, *S. scoparium*, we cannot make generalizations about non-native species richness associated with dominance by native C_4 versus non-native C_3 matrix species (Fig. 2B). This result is in contrast to the results of other studies (Crall et al. 2006, Emery and Gross 2006). Crall et al. (2006) found a positive correlation between non-native species richness and increased abundance of the non-native C_3 grass, *Bromus tectorum*. Emery and Gross (2006) found that plots dominated by the native grass species, *Andropogon virginicus*, had significantly fewer invading non-native seedlings compared to plots dominated by the non-native grass, *Bromus inermis*. Despite the approximately equal non-native species richness associated with dominance by *P. pratensis* and *S. scoparium*, our results showed that the non-native species present in *S. scoparium* dominated plots were rare

and found in very low abundances, with the exception of *P. pratensis*. Our results revealed that *P. pratensis* comprised a large proportion of the non-native cover in plots dominated by the native matrix species indicating that, even though *S. scoparium* and *A. gerardii* are the dominant species in these plots, *P. pratensis* still has a potentially strong influence on the vegetation dynamics.

The observed reduced richness with shifting dominance from native C_4 to non-native C_3 grass species has several implications. Many studies have examined the effects of reduced richness on community function and found that species richness has a significant positive relationship with community productivity (Knops et al. 1999, Haddad et al. 2000), diversity at higher trophic levels (Siemann et al. 1998, Knops et al. 1999, Haddad et al. 2000), and resource capture (Knops et al. 1999, Tilman 1999). Therefore, dominance by the non-native matrix species, *P. pratensis* and *A. repens*, could potentially be associated with poorer community function that extends into higher trophic levels.

The findings of this study are not consistent with documented successional trends of abandoned agricultural fields. Many abandoned agricultural fields undergo a succession in which the abundance and diversity of native plant species increases over time (Wali 1999, Meiners et al. 2002) and the abundance of non-native species decreases (Inouye et al. 1987, Meiners et al. 2002). We did not detect these patterns during the 23 years of this study. Instead, the relative cover of native plant species slightly decreased from 52 to 46% and native species richness decreased from 5.3 to 3.4 species per 0.5 m^{-2} (Table 1). The non-native species, *P. pratensis*, was the most dominant grass species in all sampling years and increased from 24 to 30% of the total vascular plant cover over the course of this study. This increase in the mean relative abundance and commonness of *P. pratensis* over time is a strong indication that this particular non-native matrix-forming grass is not decreasing over successional time, at least over the 24 years of our study, emphasizing the need to understand how the identity of the matrix species corresponds to the diversity of the community.

Many factors, not just one, control plant species diversity which gives justification for the low R^2 values of our analyses. While there have been many studies that have examined the role of other factors, such as nutrient availability (Tilman and Olff 1991, Vitousek et al. 1997, Clark and Tilman 2008), grazing and fire regimes (Knops 2006, Dorrough et al. 2007), and recruitment limitation (Foster and Tilman 2003, MacDougall and Turkington 2006, Zeiter et al. 2006), this study examined the less explored role of dominant species identity. Comparing our study to the results of studies that have examined the role of the aforementioned factors (Baer et al. 2003, Gross et al. 2005, Clark and Tilman 2008) highlights the importance of the role of dominant species identity. For example, Clark and Tilman (2008) examined the effects of nitrogen deposition on grassland diversity and found that low levels of nitrogen addition reduced species richness by about 17%. Our study, however, found that dominance by non-native matrix species was associated with about a 27% decrease in species richness on average compared to dominance by native matrix species. Many of the aforementioned factors not only affect community diversity, but they can also have

differential effects on species abundances (Tilman and El Haddi 1992, Baer et al. 2003) as a result of differences between species in resource requirements, stress tolerance, etc., thereby altering the competitive interactions between the species present in a community. Therefore, because factors such as nutrient availability, disturbance, climatic variations, etc. play a significant role in determining plant community diversity and also influence species abundances, including abundance of the dominant species, there is a strong need for more focus on the role of dominant species identity, especially since we are seeing a shift in dominance from native C_4 to non-native C_3 grass species in many of our grassland systems (Tyser 1992, Chapin et al. 2000, Chornesky and Randall 2003). It is important to stress that this study presents purely correlational results. These correlational observations are useful in giving insight into what factors may be influencing species richness in grassland communities but no conclusions can be made about what mechanisms are driving the observed patterns. Controlled experiments where the identity of the dominant species is actually manipulated (Wilsey and Potvin 2000) would be necessary in order to investigate the mechanisms responsible for the patterns observed between the different dominant species.

In summary, our results suggest the identity of the dominant matrix-forming species plays an important role in determining overall diversity by having a strong influence on the sub-dominant plant community. We found that *P. pratensis*, a non-native C_3 matrix grass species, was the most abundant and common species in the Cedar Creek old fields and that dominance by the non-native C_3 matrix species was associated with lower overall species richness and lower native species richness relative to dominance by the native C_4 matrix-forming grass species. Our correlational study is consistent with other studies, both correlational and experimental, and supports the generality that high non-native C_3 grass abundance corresponds with lower species richness (Wilson and Belcher 1989, Christian and Wilson 1999, Gabbard and Fowler 2007) and lower native species richness (Cleland et al. 2004).

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Supplementary material (available online as Appendix O17718 at <www.oikos.ekol.lu.se/appendix>). Appendix 1.