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Estimating floristic integrity in tallgrass prairie

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ARTICLE INFO

Article history:
Received 8 September 2005
Received in revised form
27 January 2006
Accepted 9 February 2006
Available online 5 April 2006

Keywords:
Tallgrass prairie
Restoration
Floristic quality index
Mean coefficient of conservatism
Diversity indices
Vegetation integrity
Assembly and response rules

ABSTRACT

Indices are needed in habitat conservation and restoration to provide repeatable measures relevant to conservation goals. A monitoring and research program was established at Nachusa Grasslands in north-central Illinois (USA) to assess progress in tallgrass prairie restoration and reconstruction efforts and evaluate the effectiveness of indices used to measure community-level properties related to vegetation integrity. Indices selected for comparison included standard diversity measures (e.g., Shannon–Weiner Index, Evenness, Species Richness) and indices developed specifically to estimate vegetation integrity. These latter indices included two unweighted diversity indices, the Species Richness Index and Native Richness Index, and two indices weighted by characteristics of species composition, the Floristic Quality Index (FQI) and its component Mean Coefficient of Conservatism (Mean C). A coefficient of conservatism (CC) is an integer ranging from 0 to 10 assigned a priori to each taxon in a regional flora that estimates the fidelity of a species to natural areas (non-native and most ruderal species are assigned 0 or low values, respectively; species known primarily from natural areas are assigned higher values). All indices compared in this study were calculated using vegetation data collected from equal-sized sampling grids stratified across seven prairie units. The units included remnants and plantings representing a wide range of habitat quality. The FQI and Mean C explained the most variation among sites and were most effective at distinguishing recognized qualitative differences indicating they can be more informative than traditional species-diversity measures in assessing floristic integrity within community types. The FQI and Mean C are applicable to both quantitative ecological monitoring and plotless survey methods.

1. Introduction

In the contemporary fragmented landscape, the quality of remnant native plant communities within a region can range from fairly undegraded to highly modified and degraded. While there is some consensus on the properties that characterize ecosystem or biological integrity (Munn, 1993; Angermeier and Karr, 1994), agreement on how integrity should be measured is lacking (Keddy et al., 1993) and sufficient data for a comprehensive assessment of all salient ecosystem factors and interactions rarely exists (Ulanowicz, 2000). Natural area identification and ecological monitoring are two areas in applied conservation biology where a variety of indices have been used to characterize plant communities. Typically, measured parameters have included species richness and diversity (Palmer, 1995; Sluis, 2002), functional group richness and traits (Díaz et al., 1999; Symstad, 2000; Mason et al., 2003), community structure in terms of physiognomic and compositional characteristics (Taft, 2003), and proportion of native and non-native species (Cully et al., 2003).

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0006-3207/$ - see front matter
doi:10.1016/j.biocon.2006.02.006

While measures of species diversity and richness offer a direct means to make comparisons among sites and time intervals, these parameters ignore differences in composition (Botta-Dukát, 2005) and alone may not be adequate to assess habitat integrity (Keddy et al., 1993) or progress in restoration efforts. For example, it is conceivable that habitats considered to have a high degree of natural quality (i.e., relatively undegraded by anthropogenic activities) could have similar species richness compared to similar-sized sites with highly modified or degraded vegetation. Although the sites may be exposed to similar abiotic conditions, they may differ considerably in species composition with the degraded sites dominated by ruderal species and the other dominated by species commonly associated with habitat remnants.

There is a need for simple yet sensitive and ecologically meaningful methods of classifying vegetation according to levels of ecological integrity that are repeatable, dispassionate, and can be readily interpreted, particularly by the non-specialist (Grime, 1974). In addition, a rapid method of assessment often is needed, especially when evaluating large portions of a landscape. To fill this need, diversity indices weighted by characteristics of species composition have had an increasing role in habitat assessment in recent years (Oldham et al., 1995; Majer and Beeston, 1996; Admiraal et al., 1997; Francis et al., 2000; Rooney and Rogers, 2002; Lopez and Fennessy, 2002; Bernthal, 2003; Matthews, 2003; Glennon and Porter, 2005). For vegetation studies, these indices include the Floristic Quality Index and its component the Mean Coefficient of Conservatism (Swink and Wilhelm, 1994). These indices, defined in detail in the Methods section, involve average conservatism ranks in a species pool where the coefficients of conservatism have been pre-assigned in a regional flora (e.g., Taft et al., 1997).

There are arguments for and against the weighting of species. Arguments against hinge on the initial subjectivity involved. Arguments in favor include the view that information could be gained by not counting as equal contributors to diversity a ruderal species such as *Ambrosia artemisiifolia* and a species limited to habitat remnants such as *Sporobolus heterolepis*. Or, borrowing from a similar thought though with a more evolutionary perspective, should a species of *Taraxacum* be counted equally to *Welwitschia* (Vane-Wright et al., 1991)? Weighted indices involving the Floristic Quality Index and Mean Coefficient of Conservatism have been found to be negatively correlated to gradients of disturbance in wetlands in Ohio (Lopez and Fennessy, 2002) and North Dakota (DeKeyser et al., 2003) and were considered reliable indicators of wetland plant community integrity. Further testing is needed to determine whether these indices are effective in assessing the integrity of non-wetland terrestrial plant communities.

A vegetation monitoring and research program was established at Nachusa Grasslands, a site in north-central Illinois owned by The Nature Conservancy. One of the primary goals of the program was to test the effectiveness of different indices at discriminating differences in habitat quality in tallgrass prairie communities. Comparisons of species-weighted indices to standard diversity metrics can reveal whether weighted indices provide novel information and determine whether they are justified for conservation programs, ecological monitoring, site comparisons, and hypothesis testing in restoration or reconstruction projects. Thus, the central question explored in the study was whether the weighted indices Floristic Quality Index and Mean Coefficient of Conservatism were more effective at detecting qualitative differences between and among the prairie remnants and plantings than more direct measures of species diversity.

2. Methods

2.1. Study area

Nachusa Grasslands is an approximately 627 ha habitat complex including prairie, savanna, woodlands, and wetlands at the border of Lee and Ogle counties in northern Illinois (41°53′N latitude, 89°20′50″W longitude). The site mostly is underlain by St. Peter Sandstone, a fragile Ordovician-aged formation that outcrops locally on site and readily weathers to a sandy residuum. Portions of the preserve are characterized by silt-loam or sandy-loam soils where this sandstone substrate is buried more deeply by glacial outwash and loess deposits. The preserve includes about 81 ha of natural community remnants; the remaining areas include lands previously developed for agriculture and have been the focus of habitat reconstruction efforts using seed primarily collected from the prairie remnants. The resulting native grassland complex, among the largest in Illinois, contains a great diversity of prairie species including several rare grassland bird, arthropod, and plant species.

2.2. Site descriptions and vegetation sampling

Three prairie remnants and four prairie plantings (reconstructions) were selected for study based on condition and configuration. Sites were selected that represented the range in perceived habitat quality at Nachusa Grasslands while accommodating a sampling design that, for the purposes of baseline and long-term monitoring and application of one of the diversity indices (NRI and SRI; defined later in Section 2), required multiple parallel transects, each 80–100-m long. The remnants, known as Doug's Knob, Dot's Knob, and Isabel's Knob, were selected because observers recently assigned them to three different quality classes, grades A, B, and C, respectively, using the grading criteria of the Illinois Natural Areas Inventory (INAI). The INAI grading criteria are based on perceived successional state of vegetation with grades ranging from A (essentially undegraded) to E (highly disturbed [i.e., cropland]). Sites judged as high-quality natural areas (graded A or B) total only about 0.07% of the state's land area (White, 1978). All three remnants were grazed by livestock in the past; Isabel's Knob had a history of intensive grazing while Doug's Knob and Dot's Knob were grazed less intensively. Isabel's Knob has been treated with prescribed fire nearly annually for about 20 years while the other two remnants have had periodic dormant-season fires and intervening years of no burn (T. Bittner, Illinois Department of Natural Resources, pers. comm.). For this study, to distinguish between restoration of remnants and plantings, management of remnants designed to improve habitat quality is considered restoration while plantings are considered reconstructions.

Plantings (with year of establishment) included the Main Unit (1991), Potholes Unit (1992), East Heinkle Unit (1995) and Hotchkiss Unit (1998). Precise details of seed mixes used are not available for all plantings and repeated seeding has occurred at some units.

Study units occur on soils derived from two major parent material types. Three units (Doug's Knob, Dot's Knob, and the Hotchkiss Planting) occur on soils derived from weathered sandstone; the remaining sites occur on soils derived primarily from loamy to sandy glacial outwash (Acker et al., 1980; Zwicker, 1985).

Six transects, 80–100-m long depending on site configuration, were stratified across each sample unit yielding a total sample of 42 transects and 840 quadrats (18 transects and 360 quadrats among remnants and 24 transects and 480 quadrats among plantings). End points of each transect were marked with metal fence posts. The beginning point of this stratified grid was determined randomly (stratified-random sampling). Each transect was sampled with 20 50 cm × 50 cm quadrats, oriented on alternating sides of the transect, with quadrat placement every 4 or 5 m for the 80 and 100-m transects, respectively. Within each quadrat, all vascular plant species rooted within the quadrat frame were recorded. A cover value was assigned to each taxon using a modified Daubenmire cover class system (seven classes with %-cover midpoints 0.5, 3, 15, 37.5, 62,5, 85, and 97.5). Importance values (IV 200) were calculated for each species as sum of relative frequency and relative cover. Vegetation sample data were collected from 12 June to 22 July 2001. Botanical nomenclature follows Mohlenbrock (1986).

2.3. Indices terms and definitions

The community-level indices used in this study for evaluating natural quality are listed and defined below. For data analyses (see following section), the relevant sample areas for these indices ranged in scale from quadrat to transect and site.

2.3.1. *Indices based on standard community-level emergent properties*

Adventive Species Richness = Total number of non-native (exotic) species.
Evenness = H'/ln(richness) (Gurevitch et al., 2002). Adventive species were excluded.
Shannon–Wiener Index of Diversity $(H') = -\sum[p_i \ln(p_i)]$ (Whittaker, 1975); p_i is relative importance value of each species. Adventive species were excluded.
Simpson's Index of Dominance $(D) = \sum p_i^2$ (Whittaker, 1975); p_i is relative importance value for each taxon in the sample area (transect or site). Adventive species were excluded.
Species Density = Species richness per quadrat. Adventive species were excluded.
Species Richness (S) = The number of native species in a sample area (transect or site).

2.3.2. *Unweighted indices of floristic integrity*

Native Richness Index (NRI) = $Rn(\sqrt{N})$; Rn = native species richness (density) per quadrat and N is native species richness (Bowles et al., 2000). NRI also can be calculated using log-transformed N.
Species Richness Index (SRI) = $R(\sqrt{S})$; R = species density per quadrat and S is total species richness. SRI includes all species, including adventive taxa, in the calculation of R and S (Bowles et al., 2000). Both the NRI and SRI were designed for use with transect data and 20 stratified quadrats (Bowles et al., 2000) thus setting the minimum standard for equalizing sampling intensity for all indices employed.

2.3.3. *Weighted indices of floristic integrity*

Mean Coefficient of Conservatism (Mean C) = $\sum CC/S$. CC = Coefficient of Conservatism; S = total species richness (including adventive species). Mean C also can be calculated as $\sum CC/N$, using native species only (Native Mean C [Mean C_n]).
Floristic Quality Index (FQI) = Mean $C(\sqrt{N})$; Mean $C = \sum CC/S$. N = native species richness, S = native and adventive species richness. FQI also can be calculated as Native Mean $C(\sqrt{N})$, using native species only (FQI_n).

The Mean Coefficient of Conservatism and Floristic Quality Index were developed as a hypothetical tool for evaluating floristic integrity in Illinois (Taft et al., 1997). The Coefficient of Conservatism (CC) is an integer from 0 to 10 assigned to each taxon in the Illinois flora. All non-native species were assigned values of 0. As a guide to the assignment of the C values, three species groups roughly corresponding to the C–S–R model (Grime, 1974; Grime et al., 1988) provided the general framework. For the assignment of the coefficients for the Illinois flora, species perceived as having a ruderal ecology were ranked with C values from 0 to 3. Competitors (and matrix species of plant communities) were ranked with C values from 4 to 6 while the stress tolerators were reclassified as remnant-dependent species (similar to Panzer et al., 1995) and ranked with C values from 7 to 10 (Taft et al., 1997). "Remnant-dependent species" was a more apt description than "stress tolerators" for the broad range of physiognomic and functional groupings included in this latter category.

2.4. Data analysis

For each index tested, mean comparisons of the remnant ($n = 3$) and planting ($n = 4$) sample groups were made based on indices calculated or averaged at the site scale using two-sample t-tests (H_O: remnant = planting). The probability of multiple tests yielding significant results by chance was examined with the Bernoulli equation (Moran, 2003). Variance ratio tests (Zar, 1999) indicated variance could be pooled for each comparison.

To compare and contrast sensitivity of indices within and between sample groups, variation among transect-level means was evaluated with ANOVA; planned post hoc comparisons were made with the Tukey HSD test. Relationships among selected habitat quality indices (e.g., NRI and FQI) were examined with correlation analysis. Tests of normality for indices and parameters were conducted with the one-sample Kolmogorov–Smirnov test. The above statistical testing was done with the Systat Statistical Software package, vol. 9.0 (SPSS, 1999).

Variation of species composition between sites and biotic indices and parameters were analyzed with Canonical Correspondence Analysis (CCA) using CANOCO 4 (ter Braak and Smilauer, 1998). For the CCA, the 50 top-ranking species based on importance values from the 42 transects were selected with scaling set for inter-species distances. The ordination was analyzed using a split-block design treating sites as blocks. Statistical significance of fitting CCA axes to the relationship depicted between the species and external variables (i.e., indices) was tested using a global permutation test (Monte-Carlo test) of the species data at 1,000 iterations. Forward selection of the external variables tested with Monte-Carlo permutations also was used in determining statistical significance for each index singly (marginal effects) and in order of additionally explained variance (conditional effects).

Replication for the ANOVA used in this study is within sites, rather than across sites, because there were no replicates at Nachusa Grasslands for the quality and planting-age categories. The primary interest in this study was a relative comparison of the capacity for indices to discriminate differences among sites representing a range of habitat quality. Management and protection priorities rely on indices for tracking progress in restorations and in setting benchmarks for comparison with other sites. A Monte-Carlo permutation test of within-site variability with CANOCO (using a split-plot design holding blocks [sites] unpermuted and permuting transects within sites) indicated in a test for all four canonical axes that there were statistically significant differences (F-ratio = 6.422, P = 0.01) lending support for treating transects as independent variables within sites.

3. Results

Among all sites, Native Species Density ranged from 4.4 to 9.6, Native Species Richness ranged from 38 to 63 species, and Adventive Species Richness ranged from 6 to 29 species. The remnant and planting sample groups differed in several species richness and diversity indices and parameters (Table 1). For six of 14 indices tested (FQI, FQI_n, Native Species Richness, Mean C, Native Mean C, and Adventive Species Richness) the differences were significant ($P < 0.05$). The probability of finding six significant tests out of 14 by chance is $P < 0.0001$ (Bernoulli equation). All indices, other than Dominance and Adventive Species Richness, ranked the remnant sample group higher than the planting sample group.

A comparison of transect means with ANOVA indicated significant differences existed among all sites for all indices measured ($P < 0.00001$). Pair-wise comparisons with Tukey HSD tests indicated that differences existed both among and between sites in the remnant and planting sample

Table 1 – Summary variables for vegetation sample units at Nachusa Grasslands

	Remnants				Plantings					t Stat.	P
	Doug's Knob	Dot's Knob	Isabel's Knob	Mean	Main Unit	Potholes Unit	East Heinkle	Hotchkiss	Mean		
Floristic summary data											
Native species richness	63	63	61	62.33	49	38	53	41	45.25	−4.12	0.009
Adventive species richness	8	13	6	9.00	14	17	26	29	21.50	2.74	0.041
Native species density/quadrat	8.12	7.19	9.61	8.31	8.07	4.43	7.17	5.37	6.26	−1.79	0.134
Total species richness	71	76	67	71.33	63	55	79	70	66.75	−0.71	0.507
Percent native	88.7	82.9	91.0	87.56	77.8	69.1	67.1	58.6	68.13	NA	NA
Plant family number	27	24	25	25.33	15	18	27	22	20.50	NA	NA
Community diversity metrics											
Evenness	0.810	0.802	0.774	0.796	0.787	0.643	0.749	0.839	0.755	2.09	0.091
Shannon diversity index (H' native spp)	2.876	2.771	2.668	2.771	2.628	1.967	2.596	2.635	2.456	−1.58	0.176
Simpson's dominance index (all spp)	0.074	0.071	0.119	0.088	0.102	0.192	0.083	0.058	0.109	0.56	0.600
Simpson's dominance index (native spp)	0.083	0.090	0.128	0.100	0.122	0.253	0.134	0.098	0.152	0.21	0.846
Floristic integrity indices											
Floristic quality index (FQI)	35.77	27.26	33.34	32.12	22.78	15.80	13.09	12.99	16.16	−4.63	0.006
Floristic quality index (native spp.)	40.32	32.88	36.62	36.61	29.29	22.87	19.51	22.18	23.46	−4.32	0.008
Mean C	4.51	3.43	4.27	4.07	3.25	2.56	1.80	2.03	2.41	−3.54	0.017
Native mean C	5.08	4.14	4.69	4.64	4.18	3.71	2.68	3.46	3.51	−2.59	0.049
Native richness index (NRI)	64.42	57.04	75.04	65.50	56.47	27.33	52.17	34.36	42.58	−2.45	0.058
Species richness index (SRI)	77.45	79.64	83.97	80.35	72.56	46.66	97.18	87.92	76.08	−0.33	0.759
INAI Grade	A	B	C								

INAI, Illinois Natural Areas Inventory. T statistic is from two-sample t-tests comparing site-level means among the remnant (n = 3) and planting (n = 4) sample groups at Nachusa Grasslands (df = 5).

groups. The most sensitive indices, based on the number of comparisons found to be statistically different, were Mean C followed by Native Mean C and FQI (Table 2). The least sensitive indices at detecting site differences within and between sample groups were the Shannon–Weiner Index of Diversity (H') followed by Native Species Richness and Species Richness Index (SRI). Adventive Species Richness, Native Richness Index (NRI), and Native Species Density had intermediate levels of sensitivity (Table 2).

Mean C and FQI were the indices most successful at detecting pairwise differences between individual remnant and planting sites, distinguishing 11 of the 12 possible comparisons (Table 2). One planting, the Main Unit (the oldest planting, established in 1991), had a similar Mean C and FQI compared with one remnant (Dot's Knob); all other remnant-planting comparisons were significantly different. Native Mean C and Adventive Species Richness distinguished 10 comparisons. Most all other indices and diversity measures (H', Dominance, Evenness, SRI, NRI, Native Species Richness, Species Density) distinguished 5–8 of the possible 12 remnant-planting comparisons (i.e., these indices were about 42–67% successful in distinguishing a prairie planting from a remnant). Mean C, Native Mean C, and Evenness were most sensitive at detecting differences among plantings, while Mean C, Native Mean C, FQI, Dominance, and Species Density were most sensitive at detected differences among remnants (Table 2). NRI and FQI/Mean C rank remnants somewhat differently with NRI ranking Isabel's Knob highest while FQI/Mean C ranked Doug's Knob highest (Table 1). Most indices ranked Dot's Knob lowest among remnants. SRI ranked highest the two most recent plantings (East Heinkle and Hotchkiss units).

Two indices designed specifically for estimating habitat integrity, FQI and NRI, were correlated ($r = 0.68$, df = 838, $P < 0.000001$). However, for a given NRI score, the tendency was for remnant quadrats to reach a higher FQI score than planting quadrats (Fig. 1). The differences in paired comparisons between the remnant and planting sample groups (Table 1) were greatest for the weighted index (FQI) compared to the unweighted index (NRI). NRI, by ranking sites indiscriminately according to patterns of species richness, scores the two newest plantings (East Heinkle and Hotchkiss units) comparatively higher than FQI (Fig. 2).

The results from the Tukey post hoc tests are supported by the Canonical Correspondence Analysis (CCA). Axis 1, explaining 32% of the variance in the species to diversity index relations (F-ratio = 8.66, $P = 0.009$, based on 1000 Monte-Carlo permutations), is strongly correlated with biplot scores for Mean C, FQI, and Adventive Species Richness (Table 3), albeit in opposite orientations in the ordination (Fig. 3). The results from forward selection of environmental variables

Table 2 – Summary of differences in tested floristic indices and community parameters within and between remnant and planting sample groups at Nachusa Grasslands

	Remnants	Between	Plantings	Total
Total possible comparisons	3	12	6	21
Mean C	2	11	5	18
Native mean C	2	10	5	17
FQI (all spp.)	2	11	4	17
Adventive species richness	0	10	4	14
Species density	2	8	4	14
NRI	1	8	4	13
Dominance	2	6	4	12
Evenness	0	6	5	11
Native species richness	0	7	3	10
SRI	0	6	4	10
H' (native spp.)	0	5	3	8

Differences tabulated were those considered statistically significant ($P < 0.05$) by the Tukey post hoc test.

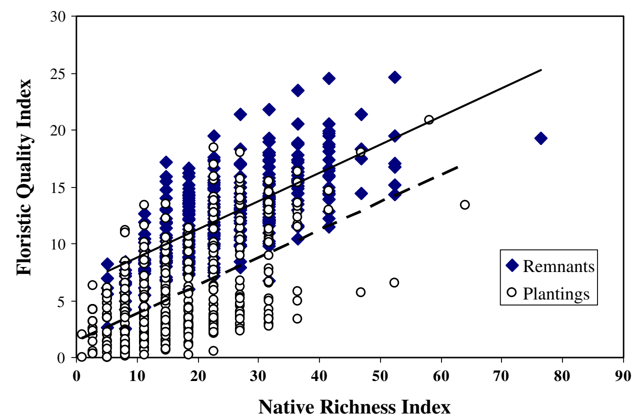

Fig. 1 – Correlation of Floristic Quality Index (FQI) and Native Richness Index (NRI) contrasting quadrats from prairie remnant ($n = 360$) and prairie planting ($n = 480$) sample groups at Nachusa Grasslands. Dashed line smoother passes through prairie planting sample group.

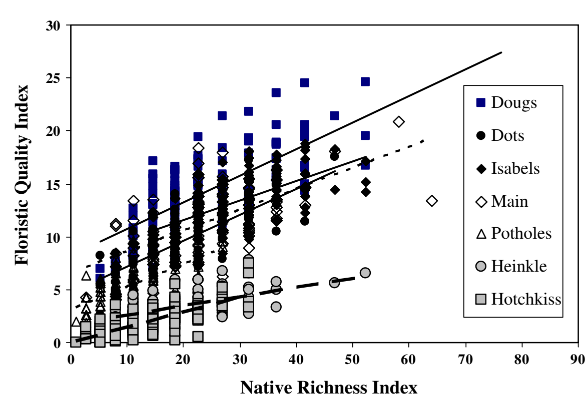

Fig. 2 – Correlation of Floristic Quality Index and Native Richness Index at Nachusa Grassland comparing trends among sites. Dots, Dougs, and Isabels are prairie remnants; other sites are plantings. Dashed line smoothers identify data from the two most recent plantings, the East Heinkle and Hotchkiss units.

Table 3 – Results from canonical correspondence analysis are shown

Axes	1	2	3	4	Total inertia
Axis loadings					
Eigen values	0.540	0.450	0.291	0.171	2.472
Species-environment correlations	0.980	0.955	0.915	0.856	
Cumulative percentage variance					
of species data	21.8	40.0	51.8	58.7	
of species-environment relation	32.4	59.4	76.8	87.0	
Species scores					
Aster sericeus	**−1.3194**	−0.5290	**1.3624**	−0.1434	
Sporobolus heterolepis	**−1.3142**	−0.5214	**1.5197**	0.1380	
Coreopsis palmata	**−1.2320**	−0.5235	**1.2742**	−0.0120	
Stipa spartea	**−1.2311**	−0.4633	**1.4304**	0.0229	
Helianthns occidentalis	**−1.2061**	−0.4440	**1.1076**	−0.1083	
Sisyrinchium campestre	**−1.0937**	−0.2362	−0.6954	−0.6753	
Dichanthelium villosissimum	**−1.0001**	−0.1787	−0.6865	−0.5036	
Viola fimbriatula	−0.9750	−0.1706	**−1.0109**	−0.5832	
Ambrosia psilostachya	−0.0483	**1.2237**	0.4824	−0.2970	
Penstemon digitalis	0.2256	**1.3726**	0.0116	−0.1339	
Andropogon gerardii	0.3895	**1.7084**	0.3128	−0.0082	
Cirsium discolor	0.6962	−0.3957	−0.6937	**1.2396**	
*Setaria viridis**	0.9935	−0.6862	−0.6806	**1.1714**	
*Taraxacum officinale**	**1.1129**	−0.0008	0.3379	−0.1730	
Ambrosia artemisiifolia	**1.1371**	−0.7957	−0.1908	0.4723	
*Daucus carota**	**1.1373**	−0.7691	0.3819	−0.3466	
*Bromus inermis**	**1.1982**	−0.7105	0.5531	−0.6250	
Asclepias syriaca	**1.2103**	−0.7091	0.4595	−0.4319	
*Trifolium pratense**	**1.2307**	−0.7795	0.2133	−0.0896	
*Chenopodium album**	**1.3925**	−0.6798	0.6019	−0.4326	
Calystegia sepium	**1.5641**	−0.9664	0.6647	−0.6935	
*Medicago sativa**	**1.6270**	**−1.1125**	0.8132	−0.9884	
Biplot scores of environmental variables					
FQI	**−0.9688**	−0.0872	0.1811	−0.0595	
MeanC	**−0.9642**	0.0216	0.1853	−0.1183	
NRI	**−0.7615**	−0.4220	−0.3968	0.0196	
Species density	**−0.7201**	−0.4354	−0.4967	−0.1214	
Native species richness	**−0.6810**	−0.4194	−0.1059	0.3376	
H′	−0.4332	**−0.7921**	0.0217	0.0101	
Evenness	−0.1566	**−0.8262**	0.1165	−0.2846	
SRI	0.0780	**−0.7877**	−0.3310	0.2474	
Dominance	0.3065	**0.8270**	−0.0855	0.0457	
Adventive species richness	**0.9363**	−0.2653	−0.0105	0.1133	

For species scores, data are based on Importance Value (using the top 50-ranking species), and for "environmental variables", data are diversity indices. Bold indicates prominent species and biplot scores. * adventive species. Ordination scaling is inter-species distances. Only species with scores >1.0 on one of the axes are shown (complete species list available upon request).

indicate that most variance in the species data, when examined singly (marginal effects), was explained by FQI, Mean C, and Adventive Species Richness (Table 4). The conditional effects, the variation explained by environmental variables in order of their inclusion in the model, the additional variance each variable explained at the time it was included (lambda-A), and the significance of the variable at that time (*P*-value), indicate that only FQI and Mean C explain significant portions of the variation in the data. Treating transects as fully independent yielded statistical significance for all indices except Dominance, SRI, and Species Richness (Table 4).

Species associations among transects and sites (Fig. 3) show mainly ruderal species associated with the newest plantings (species with positive biplot scores [Table 3]) and prairie species associating with the remnants (species with negative biplot scores [Table 3]). Species scores on the first axis plotted against Coefficients of Conservatism for species in the ordination yielded a significant inverse correlation ($r = 0.8$, df = 48, $P < 0.00001$).

Indices scoring highly on Axis 2 were Dominance, Evenness, H', and SRI. NRI, Species Density, and Native Species Richness show covariance in ordination space and are intermediate in the ordination between SRI and FQI. Site rankings on the second axis of the ordination do not discriminate recent plantings from remnants (Fig. 3).

4. Discussion

The seven prairie units selected for this study represent a range of habitat condition from relatively undegraded rem-

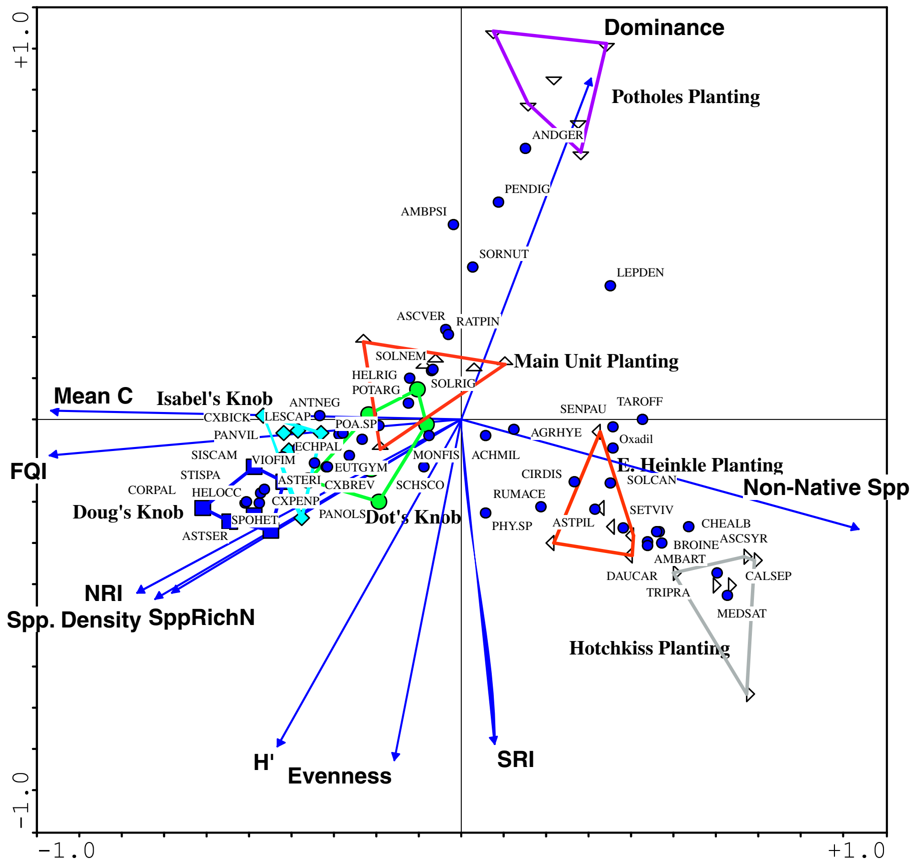

Fig. 3 – Ordination of species, sites, and diversity indices on Axis 1 and Axis 2 of a Canonical Correspondence Analysis (CCA) with scaling based on inter-species distances. Each "plot" within a site represents transect-level summary data based on importance value for the top ranking 50 species. Remnants are shown with solid symbols and plantings with open symbols. Acronyms for species are first three letters of genus and species. Envelopes include sample points (transects) for each site. ACHMIL, *Achillea millefolium*; AGRHYE, *Agrostis hyemale*; AMBART, *Ambrosia artemisiifolia*; AMBPSI, *Ambrosia psilostachya*; ANDGER, *Andropogon gerardii*; ANTNEG, *Antennaria neglecta*; ASCSYR, *Asclepias syriaca*; ASCVER, *Asclepias verticillata*; ASTERI, *Aster ericoides*; ASTPIL, *Aster pilosus*; ASTSER, *Aster sericeus*; BROINE, *Bromus inermis*; CALSEP, *Calystegia sepium*; CHEALB, *Chenopodium albidum*; CIRDIS, *Cirsium discolor*; CORPAL, *Coreopsis palmata*; CXBICK, *Carex bicknellii*; CXBREV, *Carex brevior*; CXPENP, *Carex pensylvanica*; DAUCAR, *Daucus carota*; ECHPAL, *Echinacea pallida*; EUTGYM, *Euthamia gymnospermoides*; HELOCC, *Helianthus occidentalis*; HELRIG, *Helianthus rigidus*; LEPDEN, *Lepidium densiflorum*; LESCAP, *Lespedeza capitata*; MEDSAT, *Medicago sativa*; MONFIS, *Monarda fistulosa*; OXADIL, *Oxalis dillenii*; PANOLS, *Dichanthelium oligosanthes*; PANVIL, *Dichanthelium villosissimum*; PENDIG, *Penstemon digitalis*; POA.SP, *Poa pratensis/compressa*; POTARG, *Potentilla arguta*; RATPIN, *Ratibida pinnata*; RUMACE, *Rumex acetosella*; SCHSCO, *Schizachyrium scoparium*; SENPAU, *Senecio pauperculus*; SETVIV, *Setaria viridis* SISCAM, *Sisyrinchium campestre*; SOLCAN, *Solidago canadensis*; SOLNEM, *Solidago nemoralis*; SOLRIG, *Solidago rigida*; SORNUT, *Sorghastrum nutans*; SPOHET, *Sporobolus heterolepis*; STISPA, *Stipa spartea*; TAROFF, *Taraxacum officinale*; TRIPRA, *Trifolium pretense*; VIOFIM, *Viola fimbriatula*.

nants to recently planted reconstructions. The average Coefficient of Conservatism (Mean C) and its weighted index of diversity, Floristic Quality Index (FQI), were the most sensitive indices tested at differentiating levels of habitat quality. These study results indicate that the proportion of species classified as ruderal, matrix, and remnant-dependent (Taft et al., 1997) provides a more precise estimate of habitat integrity when compared with direct indices of species richness or diversity. Based on principles of deletion and addition response rules for communities (Keddy, 1992), it is predicted that as the forces that lead to habitat degradation increase, Mean C and FQI will decline as remnant-dependent species intolerant of the new disturbance levels are extirpated and species tolerant of the new levels of disturbance (e.g., ruderal species) increase proportionately in the species pool.

We make the following conclusions from these results. If the interest of a vegetation assessment or monitoring program concerns spatial or temporal differences in species richness or diversity, many of the unweighted diversity indices (e.g., Native Species Richness, Species Density) can be recommended. The Native Richness Index (NRI) ranked the remnant sample group over the planting sample group, but did not consistently distinguish sites among or between these groups. Several other indices unweighted by species composition (Species Richness Index [SRI], Dominance, H', and Evenness), while explaining some of the variance in the data,

Table 4 – Summary of global permutation test (1000 Monte-Carlo permutations) and results of forward selection of diversity indices

Marginal effects		Conditional effects				
Variable	Lambda 1	Variable	Lambda A	*F*-value	P_1	P_2
Forward selection results						
FQI	0.52	FQI	0.52	10.67	**0.001**	**0.001**
Mean C	0.51	*H′*	0.37	9.01	0.068	**0.001**
Adventive spp. richness	0.51	Species Density	0.27	7.97	0.070	**0.001**
NRI	0.44	Evenness	0.13	3.95	0.306	**0.001**
Species density	0.44	Adventive spp. richness	0.10	3.26	0.212	**0.006**
H′	0.40	Dominance	0.05	1.77	0.168	0.067
Dominance	0.38	SRI	0.05	1.77	0.110	0.09
Evenness	0.36	NRI	0.06	2.14	0.072	**0.039**
Species richness	0.36	Mean C	0.10	3.70	**0.013**	**0.004**
SRI	0.33	Species richness	0.02	0.84	0.521	0.568

Forward selection test results show relation between species and bioindicators with Canonical Correspondence Analysis. Sites were treated as blocks for permutations (P_1); as an alternative, results are shown treating transects as independent for permutations (P_2). Marginal effects rank variables according to the variance explained singly; conditional effects show the variation explained by the diversity indices in the rank order of their inclusion in the model.
Summary of global permutation test. Test of significance of first canonical axis: eigenvalue = 0.540; F-ratio = 8.657; P = 0.009. Test of significance of all canonical axes: Trace = 1.668; F-ratio = 6.422; P = 0.001.

appear to be independent of differences in vegetation integrity. SRI ranked the two recent plantings highest among all sample units since non-native species prevalent at these sites increase the index. Consequently, SRI is an imprecise indicator of natural quality since diversity or abundance of exotic plant species have been correlated with habitat degradation (White, 1978; McKnight, 1993; Luken, 1997) and lowered habitat integrity (Angermeier, 1994; Angermeier and Karr, 1994).

Patterns of exotic species diversity and abundance involve many factors and are scale and habitat dependent (Stohlgren et al., 2003; Brown and Peet, 2003). These patterns have shown both positive and negative association with native species richness (Stohlgren et al., 1999). When making comparisons within a community type and where differences in resource availability do not greatly differ, existing richness patterns of adventive species appear to be more explained by interactions among site factors such as disturbance and propagule availability (Shea and Chesson, 2002; Brown and Peet, 2003) than richness of native species. Ruderal natives absent or in low abundance at undegraded remnants but present in disturbed sites of the same habitat type (e.g., *Ambrosia artemisiifolia*, *Asclepias syriaca*, and *Calystegia sepium*) respond similarly depending on propagule availability. Therefore, down-weighting adventive and ruderal species, as with the Mean C and FQI, has merit for indices designed for estimating floristic integrity.

Consequently, if the interest in a habitat conservation or monitoring program concerns measuring differences and/or changes in floristic integrity as related to the species assemblage, species-weighted indices Mean C and FQI appear to be uniquely sensitive to site qualitative differences. These findings are consistent with results from examination of wetlands using floristic quality indices that indicated wetland site scores were inversely correlated with degree of disturbance, landscape alteration, and other factors (Lopez and Fennessy, 2002; DeKeyser et al., 2003). Calculations for Mean C are recommended to include the non-native species since these lower the Mean C (and the FQI) giving a more realistic account of the integrity of the vegetation within a site. In the present study, importance of exotic species explains more variance among sites than many of the diversity indices (e.g., *H′*, Native Species Richness, Dominance, Evenness, NRI, SRI). Based on species and site scores in the ordination, the first axis is interpreted as a disturbance gradient, and Mean C and FQI serve as proxies for habitat integrity.

Floristic integrity as used here is somewhat distinct from ecological or biological integrity. Ulanowicz (2000) defines ecological integrity on the basis of four attributes: system "health", undiminished capacity, capacity of a system to change, and capacity of system to withstand stress. This can be achieved with functional redundancy in the species pool to compensate for moderate compositional shifts without losing ecosystem functions. Angermeier and Karr (1994) indicate that assessing biological integrity also should account for ecosystem processes. Thus ecological and biological integrity consider sustainability factors. At the level of the plant community, floristic integrity implies an assemblage that is relatively unchanged by anthropogenic sources of habitat degradation but does not require that the community is ecologically pliable, or capable of adapting to altered conditions.

The Illinois Natural Areas Inventory procedure for grading natural quality in prairies and other habitats (White, 1978), while largely an empirical judgment and subject to variable interpretation among practitioners, takes into account relative frequency of conservative and adventive species, total species richness, extent of woody encroachment (prairie communities), and evidence of past disturbance. With the exceptions of *H′*, Dominance, and Evenness (indices that were relatively insensitive to remnant-planting differences), no other indices ranked remnants strictly according to INAI grades. Mean C, Native Mean C, and FQI did rank Doug's Knob (Grade A) highest, consistent with INAI grading. However, these same indices ranked Isabel's Knob (Grade C) higher than Dot's Knob (Grade B) while the indices influenced by species density (NRI, SRI) ranked Isabel's Knob higher than both Doug's Knob and Dot's Knob. Fire tends to increase species density in ecotonal habitats (Taft, 2003) and the frequent applications of fire at Isabel's Knob may be responsible for locally high species density. The Main Unit ranked as the planting most similar to remnants and shared ordination space with Dot's Knob. Similarity of prairie plantings to remnants has been shown to increase with time (McLachlan and Knispel, 2005). For purposes of adaptive management, monitoring data will be needed to determine whether the other plantings ultimately converge towards greater similarity with the Main Unit and the remnants.

Based on these and other results (e.g., Lopez and Fennessy, 2002; DeKeyser et al., 2003), Mean C and FQI can provide novel insights for guiding conservation priorities and assessing trends in restoration and reconstruction efforts not found with indices that measure patterns species richness alone. Further testing will be needed to determine if such species-weighted indices serve as general assembly and response rules for other community types. FQI and Mean C have the added advantage to many diversity indices in that they also can be calculated from both plot-based and plotless sample data.

Some properties of FQI and Mean C should be understood before application. FQI, as the product of Mean C and transformed species richness, is area-dependent (Taft et al., 1997; Francis et al., 2000; Matthews et al., 2005), although among wetland community types there is variation in the degree of area dependence (Matthews, 2003). Mean C has been assumed to be mostly an area-independent metric (Taft et al., 1997; Francis et al., 2000); however, evidence from wetland studies suggest Mean C also can be positively correlated to wetland area, albeit less so than FQI (Matthews et al., 2005). This relationship may be driven by very small sites less likely to sustain some conservative species. Therefore, caution is needed when comparing sites that differ greatly in total area. Equalizing sample effort can reduce area influence in wetland communities (Matthews et al., 2005). In the present study, while the sampling was equalized across all sites, each of the plantings was larger than the remnants. The lower FQI and Mean C scores for these plantings stresses the site differences based on the integrity of the species assemblages. Seasonal differences also have been shown to influence FQI while Mean C temporally is more stable (Francis et al., 2000; Matthews, 2003). FQI, then, is most meaningful when considered in context with Mean C and survey season, area, and effort. While FQI can be useful in making appropriate site comparisons, one of the most sound applications may be in ecological monitoring. Quantitative data readily can be integrated into site analyses by totaling sum importance (or relative frequency or cover) among CC values. Comparisons of proportion profiles can be made with the Kolmogorov–Smirnov two-sample test to determine non-random differences among sites or time intervals (Taft et al., 1997).

Mean C may be insensitive when used alone to detect changes associated with prescribed fire management programs because predominant changes often involve patterns of species richness and physiognomy (Taft, 1999, 2003; Bowles and Jones, in press). A lack of change in Mean C under these circumstances can be attributed to stability in the proportion of ruderal, matrix, and remnant-dependent species. However, among the indices tested in this study, the Mean C would be the most sensitive at detecting changes from management actions that resulted in disproportionate increases or decreases in ruderal or remnant-dependent species (with or without changes in diversity). Monitoring Mean C in these cases can serve to signal problems such as emergence of ruderal species from the seed bank or off-site sources.

Acknowledgements

This work was supported by the Rodney Johnson and Katharine Ordway Stewardship Endowment of The Nature Conservancy (TNC) and support from the Illinois Department of Transportation. Much thanks to Bill and Susan Kleiman, preserve managers at Nachusa Grasslands, for their congenial cooperation, help, and accommodation during this study. Thanks also to Tim Tear, TNC, for help with the grant application. Thanks to Jeff Matthews (INHS) and anonymous reviewers who provided helpful suggestions for improvements to the manuscript.

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