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Vascular plant compositional gradients within and between Iowa fens

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Abstract

Question: What is the nature and relative importance of compositional gradients within- and between fens?

Location: Iowa, USA.

Methods: 506 0.5 m × 0.5 m quadrats were sampled from 31 fens across a 550 km extent. Presence/absence of all vascular plant taxa, plus the non-vascular genera *Sphagnum* and *Chara*, and values for 24 environmental variables were noted. Global Non-Metric Multidimensional Scaling and Monte Carlo tests were used to describe compositional variation and identify significant environmental co-variables. Model-based cluster analysis was used to identify the optimal number of groups supported by the data, while *k*-means clustering was used to assign each quadrat to a group. The number of occurrences (and frequency) of each species within each group was calculated. Two-dimensional 95% Gaussian confidence intervals, ANOVA, correlation coefficient homogeneity tests, log-linear modelling, and Fisher's exact tests were used to document patterns of compositional change.

Results: Two stable axes of variation were identified: the first being most closely correlated with soil pH, Mg, Ca, P, S, vegetation height, surface and –10 cm soil temperature, site area, perimeter, perimeter/area ratio, growing season, and air temperature, with the second being most correlated to soil moisture, N, disturbance level, % organic matter, hummock height, N-S coordinate, and precipitation. Individual sites harboured between 20-47% of total compositional variation, with 28% of Axis 1 and 55% of Axis 2 scores being contained within-sites. Five compositional regions were identified that differed in the proportion of calciphile and hydrophile species. Compositional groups differed significantly between geologic types.

Conclusions: While the principal axis of variation (corresponding to the rich-poor fen gradient) is present largely between sites, the second axis (corresponding to water level) is largely repeated within sites. Documentation and protection of vegetation patterns and species diversity within Iowa fens will thus require consideration of multiple sites across the landscape.

Keywords: Cluster analysis; Community ecology; Gradient analysis; Landscape pattern; Multidimensional scaling; North America; Peatland.

Nomenclature: Nekola (1994).

Introduction

To understand the full range of environmental factors influencing peatland vegetation, simultaneous documentation of both within- and between-site gradients must take place. Unfortunately, previous investigations have focused either on numerous (> 80) quadrats from individual sites (van der Valk 1975; Bernard et al. 1983; Stewart 1987; Singsaas 1989; Gerdol 1990; Glaser et al. 1990; Magnússon & Magnússon 1990; Mooney & O'Connell 1990; Wassen et al. 1990a; Stoynoff 1993; McCormac & Schneider 1994; Fojt & Harding 1995; Bowles et al. 1996; Choesin & Boerner 2000; Gunnarsson et al. 2000; Choesin & Boerner 2002; Southall et al. 2003), or on few (< 10) quadrats sampled from multiple sites in the landscape (Charman 1993; Johnson & Leopold 1994; Motzkin 1994; Slack 1994; Bergamini et al. 2001; Vanderpuye et al. 2002; Stammel et al. 2003). The following study considers the relative importance of compositional gradients within- and between-site fens based on moderate numbers (10-30) of quadrats sampled from multiple sites (31) across Iowa. These data will be used to address the following questions: 1. What are the major compositional gradients? 2. What environmental factors underlie these trends? 3. How much compositional variation is captured within vs. between sites?

Methods

Study region

Fens are peatland habitats with saturated (not inundated) soils whose source water has been enriched in nutrients by passage through the ground (Sjörs 1952). Fewer than 200 fens remain in the northeastern half of Iowa out of an original ca. 2400 pre-settlement sites (Nekola 1994). Extant examples are most common on the Iowan Erosional Surface and the northwestern margin of the Des Moines Lobe (Fig. 1). The Iowan Erosional Surface was formed through intense periglacial erosion during the Wisconsinan, while the Des Moines Lobe was formed ca. 14000-12000 yr ago during a final surge of Wisconsinan ice sheet following the onset of climatic warming (Prior 1991).

These fens can be broadly classified into five geological types, depending upon aquifer type (Thompson et al. 1992): glacial till, bedrock, eolian sand, fluvial sand, and former lake basins (pothole or oxbow lakes). While statistical differences exist in peat chemistry between these groups (e.g. percent organic matter, pH, P, Ca, and Mg), no more than 35% of observed variance is accounted for by them (Nekola 1994).

Study sites

In total 31 fens from 23 counties across a 550 km extent (Fig. 1) were selected for analysis based on their natural integrity and geographical location. Investigation was limited to high-quality, undisturbed sites that maximized geographic spread across the landscape. While an attempt was made to maintain at least 40 km separation, some very high-quality sites were selected even though they were more closely positioned. Selected fens represent all five major geologic groups (22 till, 4 basin, 2 bedrock, 2 eolian, and 1 fluvial) and range in size from 0.1 - 28.8 ha (Table 1).

Field methods

A total of 506 0.5 m × 0.5 m quadrats were sampled in June and July, 1989. While this quadrat size is smaller than some previous North American investigations (i.e. Motzkin 1994), it is consistent with many other peatland vegetation studies (e.g. Bellamy 1967; Singaas 1989; Magnússon & Magnússon 1990; Stoynoff 1993; Bowles et al. 1996). This grain size is adequate for ordination analysis as it captures an average of 12 co-occurring species, or ca. 15% of an individual site flora.

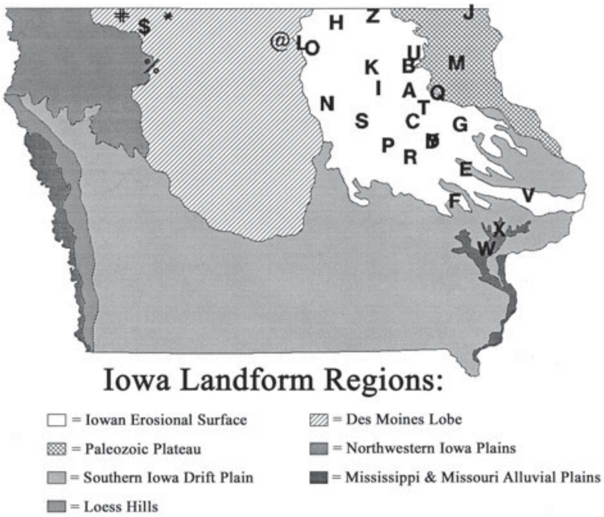

Fig. 1. Landform regions of Iowa with location of sampled fen sites. Site letter codes correspond to those in Table 1.

Sites were sampled at two intensity levels. One group (10 sites) was more intensively sampled at 30 quadrats per site. An effort was made to geographically stratify these across the landscape. At Mt. Auburn fen, only 26 quadrats were sampled due to weather conditions; 10 quadrats per site were recorded from the second group (21 sites). Only 7 and 5 quadrats were recorded from Rochester South and Rowley North, respectively, due to weather conditions.

Each site was divided into five concentric zones of equal width positioned from the centre to edge. While zone widths differed between sites, their moisture levels were similar. Stratified-random sampling was used to position quadrats within each zone. When this sampling protocol missed major vegetation types or rare species, additional quadrats were non-randomly placed to capture them. Such subjective placement was limited to less than 10 quadrats (< 2% of total).

All vascular plant species, plus *Sphagnum* and *Chara* spp., were noted from each quadrat. Surface and subsurface (–10 cm) soil temperature, vegetation height, and maximum hummock height were also recorded. Level of disturbance was noted using a subjective score ranging from 1 (least) to 3 (most). Site locations, perimeters and areas were calculated through digitization of USDA Soil Conservation Service county soil maps.

Soil chemistry

A 100-cm^3 soil sample was taken from the centre of each quadrat. These were transported in water-tight plastic bags and not allowed to come in contact with sulfur-rich paper products. Samples were either oven dried within eight hours of collection, or frozen for later drying. Following the methodologies of Dahnke (1988), percent organic matter, pH, NO_3-N, extractable P, exchangeable K, extractable SO_4-S, exchangeable Ca, and exchangeable Mg were determined by Minnesota Valley Testing Laboratory of Nevada, Iowa.

The percent water mass present in each wet sample was determined. However, because the water holding capacity of soils is positively correlated with organic matter content (Hudson 1994), many waterlogged but mineral-rich samples had lower water mass percentages than seemingly drier samples with higher organic matter levels. To help correct for this, soil moisture (*SM*) was calculated for each sample based on the following:

$$SM = W * (1 - O) \tag{1}$$

Table 1. List and locations for sampled fen sites, including their size, geologic type, sampled quadrats, and percent compositional overlap with all other sites.

County	Site name	Location	Size (ha)	Geologic type	Quadrats sampled	% overlap	Site code
Allamakee County	Clear Creek 1	91° 25' 28" W., 43° 27' 30" N.	1.3	Fluvial	11	80.4	J
Benton County	Mt. Auburn	92° 5' 59" W., 42° 14' 50" N.	28.8	Till	26	22.3	R
Black Hawk County	Hammond Road	92° 20' 36" W., 42° 20' 48" N.	1.6	Till	10	23.8	P
Bremer County	Brayton-Horsley	92° 6' 27" W., 42° 48' 35" N.	4.7	Till	30	35.7	A
	Bushing	92° 27' 1" W., 42° 49' 48" N.	2.0	Till	12	43.5	I
Buchanan County	Cutshall Access	92° 4' 17" W, 42° 32' 47" N.	4.0	Basin	10	46.6	C
	Rowley	91° 51' 7" W., 42° 22' 27" N.	2.2	Till	30	22.9	D
	Rowley North	91° 51' 5" W., 42° 22' 36" N.	0.3	Till	5	70.1	Y
Cedar County	Rochester South	91° 8' 12" W., 41° 36' 59" N.	0.3	Eolian	7	23.4	X
Cerro Gordo County	Buffalo Slough	93° 11' 54" W., 43° 10' 36" N.	12.6	Basin	30	36.6	O
	Neuhring	93° 18' 39" W., 43° 13' 3" N.	1.0	Till	10	45.8	L
Chickasaw County	Chickasaw 1	92° 31' 3" W., 43° 0' 33" N.	18.4	Till	10	65.9	K
	Kleiss	92° 6' 20" W., 43° 0' 58" N.	1.6	Till	10	28.8	B
Clay County	Gillett	95° 0' 52" W., 43° 0' 53" N.	3.1	Till	10	48.6	%
Clayton County	Postville	91° 34' 0" W., 43° 2' 3" N.	37.5	Till	10	84.7	M
Clinton County	Toronto 2	90° 48' 9" W., 41° 53' 49" N.	1.3	Eolian	30	87.0	V
Delaware County	Hawker	91° 32' 38" W., 42° 30' 47" N.	7.3	Till	30	45.6	G
Dickinson County	Silver Lake	95° 21' 55" W., 43° 26' 16" N.	2.6	Till	12	84.4	#
	Lower Gar Lake	95° 6' 34" W., 43° 20' 48" N.	3.3	Till	10	61.7	$
Emmet County	O'Brien	94° 50' 36" W., 43° 26' 16" N.	0.1	Till	10	31.5	*
Fayette County	Hunter Creek	91° 56' 50" W., 42° 39' 32" N.	0.9	Till	10	18.3	T
	Smithfield Township Hall	91° 47' 18" W., 42° 46' 57" N.	3.5	Till	30	21.2	Q
Franklin County	Maynes Creek	93° 1' 49" W., 42° 42' 24" N.	1.0	Bedrock	10	35.1	N
Grundy County	New Hartford	92° 38' 22" W., 42° 33' 16" N.	1.4	Till	10	34.7	S
Howard County	Staff Creek	92° 30' 34" W., 43° 26' 40" N.	2.4	Till	13	54.4	Z
Linn County	Matus	91° 29' 4" W., 42° 7' 57" N.	18.5	Till	30	55.9	E
	Western College	91° 37' 2" W., 41° 51' 56" N.	0.6	Till	10	31.9	F
Mitchell County	St. Ansgar	92° 55' 27" W, 43° 23' 21" N.	2.0	Bedrock	30	55.2	H
Muscatine County	Nichols	91° 16' 54" W., 41° 27' 24" N.	49.3	Basin	30	17.9	W
Palo Alto County	Dead Man's Lake	93° 33' 59" W., 43° 14' 57" N.	1.2	Basin	10	11.3	@
Winneshiek County	Jackson Juncton	92° 2' 52" W., 43° 7' 15" N.	1.4	Till	10	46.0	U

where W = percent water mass of wet soil sample; and O = percent organic mass of dry soil sample. When soil organic content is low SM remains close in value to the observed percent water mass. However, as soil organic matter content increases, SM will fall accordingly. Meaningful comparisons between sites were made possible by severe drought conditions that allowed differences to reflect differential groundwater seepage rates as opposed to timing of rainfall events.

Water chemistry was not measured for two principal reasons: First, as standing water was not present in all quadrats it could have been sampled only through the digging of pits that will cause significant alterations to water chemistry (Glaser et al. 1990). Second, soil chemistry is a much better correlate for vascular plant composition (Sjörs & Gunnarsson 2002) while water chemistry principally impacts bryophytes (Vitt & Chee 1990).

Climate analysis

Principal Components Analysis in conjunction with a varimax rotation was conducted on 30-yr mean values for 22 climate variables measured from 96 Iowa recording stations. Four major gradients, accounting for over 95% of the total climate variation, were identified: air temperature (correlated with Average Yearly, Summer, Fall, and Spring Temperatures, Heat Stress Days/Year, Heat Stress Degrees/Year, Heating Degree Days, Cooling Degree Days, Growing Degree Days), non-summer precipitation (correlated with Average Yearly, Winter, Spring and Fall Precipitation, Average Winter Temperature, Maximum 24-hr Precipitation), growing season (correlated with 32°, 30°, 28°, 26°, and 24° Growing Seasons, number of Freezing Days/Year), and average summer precipitation (Nekola 1994). PCA scores along each of these axes were determined for each recording station, with punctual kriging (Burgess & Webster 1980) being used to estimate site-specific values along each axis based upon the nearest 20 stations.

Statistical procedures

Ordination

Species lists from each quadrat were subjected to global non-metric multidimensional scaling (NMDS) using the DECODA software program (Minchin 1990).

NMDS was used as it is the most robust form of ordination for detection of ecological pattern (Minchin 1987). Using all species, a dissimilarity matrix was calculated using the Kulczynski index (Faith et al. 1987) for all pairwise combinations of sites. NMDS in one through four dimensions was then performed with 200 maximum iterations, a stress ratio stopping value of 0.999900, and a small stress stopping value of 0.010000. Output was scaled in half-change units.

Because a given NMDS run may locate a local (rather than the global) stress minimum, multiple NMDS runs starting from different initial random points must be compared to determine solution stability (Minchin 1987). For this ordination, DECODA used a total of 20 random starting configurations. Solutions in each of the four dimensions were compared using Procrustes transformations to identify those that were statistically distinct. The number of unique solutions, and runs that fell into each was then calculated across each of the four dimensions. The modal solution out of twenty runs was identified and was considered stable when it was achieved in at least 25% of starts.

Identification of compositional groups

Clustering was performed on the selected ordination output rather than raw data as the former are less susceptible to sampling or other inadvertent errors (Equihua 1990). Model-based cluster analysis (Banfield & Raftery 1992) was used to identify the number of groups most supported by the data. A sum-of-squares model was employed as it generates spherical clusters that will be of maximal compositional similarity. The approximate weight of evidence for k clusters (AWE_k) was calculated for $k = 1$ to $n–1$ clusters (where n = the total number of ordinated sites) via the *S*+ MCLUST algorithm (Anon. 1995); *k*-means iterative relocation (Hartigan 1975) was then used to assign each site to a cluster as it is also based on sum-of-squares criteria.

Ordination interpretation

The number of occurrences (and frequency) of each species within each *k*-means cluster was calculated. The 20 most frequent taxa, and rare taxa (see Nekola 1994) reaching modal frequency within each cluster, were then determined. Two-dimensional 95% Gaussian confidence intervals (Sokal & Rohlf 1981) were calculated for each site and used to estimate compositional overlap between sites. Quadrats from other sites were considered statistically similar in composition when they fell within a given site's 95% confidence ellipse. Quantification of Axis 1 and Axis 2 stand score variation between sites was accomplished via ANOVA and represented using box plots. The significance of differences in the variation accounted for between sites was estimated using a correlation coefficient homogeneity test (Sokal & Rohlf 1981).

The maximum correlation vectors for all environmental variables were calculated by DECODA and their significance estimated through Monte-Carlo tests. Variables were assigned into one of two groups: those that varied within sites (pH, NO_3-N, P, K, SO_4-S, Ca, Mg, % organic matter, vegetation height, hummock height, surface soil temperature, –10 cm soil temperature, disturbance level, soil moisture), and those that only varied between sites (N-S Coordinate, E-W Coordinate, Perimeter, Area, Perimeter/Area Ratio, Non-Summer Precipitation, Summer Precipitation, Growing Season, Air Temperature).

Significance of differences in frequency of each *k*-means cluster between the five geologic fen types was estimated via log-linear modelling. As predicted values were sparse (< 5) in more than one-fifth of cells (Zar 1984), Fisher's Exact test was used to identify those compositional clusters significantly favoured within each geologic group. Because the total number of quadrats sampled from glacial till sites exceeded 200, log-linear modelling was used to estimate significance for this group. The significance threshold for these analyses were adjusted to $p = 0.01$ using a Bonferroni correction.

Results

Site ordination

A total of 217 taxa (including *Sphagnum* and *Chara*) were identified (App. 1). NMDS demonstrated that in one dimension the most stable solution (minimum stress configuration = 0.3607) was achieved in 14 starts; in two dimensions the most stable solution (minimum stress configuration = 0.2467) was achieved in five starts; in three dimensions the most stable solution (minimum stress configuration = 0.1923) was achieved in two starts; and in four dimensions all starts provided different solutions (minimum stress configuration = 0.1594). The most stable two-dimensional solution was chosen for further analysis because it possessed a relatively low stress level while also being achieved in at least 25% of starts.

Visual observation of this solution demonstrated essentially constant variation across both axes (Fig. 2). One major outlier (from Silver Lake Fen and the lone quadrat located in a hypercalcarous water track) is present approximately 0.75 axis units to the right of the general distribution. This microhabitat is quite rare in Iowa, being limited to this and two adjacent sites.

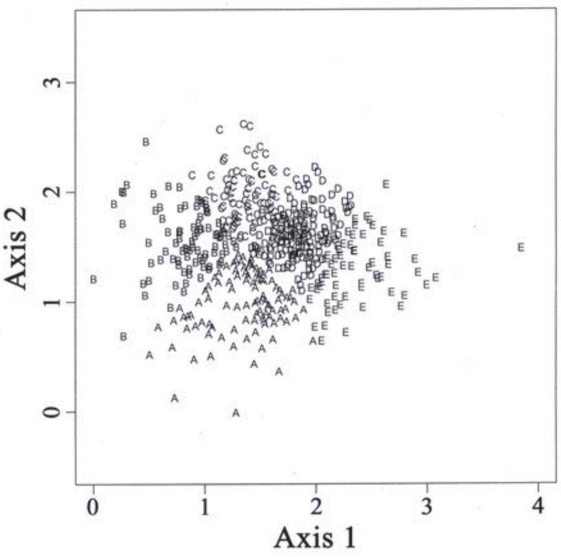

Fig. 2. NMDS ordination of 506 Iowa fen quadrats. Letters correspond to the compositional group that each quadrat was assigned via *k*-means clustering.

Compositional variation within and between sites

Considerable compositional overlap was noted between sites, ranging from 11.3% of all other quadrats (Dead Man's Lake) to 87% (Toronto 2), with a median of 43.5% (Table 1). These values are skewed slightly to the right, with the bulk ranging from 20 - 47%. ANOVA identified significant ($p < 0.0005$) partitioning of both Axis 1 and Axis 2 scores between sites. However, the amount of variance explained significantly ($p < 0.000005$) varies from 72% for Axis 1 to 45% for Axis 2 (Fig. 3).

Identification and description of compositional clusters

The maximum AWE_k score (2426.9) was achieved at 73 compositional clusters. As this represents too many groups for generalization of compositional trends, AWE_k scores from $k = 1$ to 15 were calculated, along with the percent increase in AWE_k from $k–1$ to k clusters. After six clusters, the percent increase in AWE_k fell below 10%, and decreased steadily to the 2.5% range by cluster 15. However, as the sixth *k*-means cluster contained only a single outlying quadrat (the Silver Lake fen water track), it was considered a statistical artifact with low inferential power. Each quadrat was thus assigned to one of five clusters.

Cluster A (100 quadrats) is located on the lower left of the ordination diagram (Fig. 2) and is dominated by plants such as *Campanula aparinoides, Impatiens capensis, Aster puniceus, Carex prairea*, and *Lycopus americanus* that demand high moisture levels but can tolerate non-calcareous conditions (Table 2). In this cluster 14 rare Iowa fen species reach their modal frequencies (Table 3) including *Aster junciformis, Berula erecta, Galium labradoricum, Menyanthes trifoliata, Salix pedicellaris* and *Solidago uliginosa*.

Cluster B (88 quadrats) is located in the upper left of the ordination diagram (Fig. 2) and is dominated by two ferns (*Thelypteris palustris* and *Onoclea sensibilis*) and other species such as *Polygonatum sagittatum* and *Triadenum fraseri* that can tolerate somewhat drier, non-calcareous conditions (Table 2). Four rare Iowa fen species/genera reach modal frequencies in this cluster (Table 3) including *Drosera rotundifolia, Potentilla palustris, Rubus pubescens, Sphagnum* spp. and *Triadenum fraseri*.

Cluster C (85 quadrats) is located in the upper centre of the ordination diagram (Fig. 2) and is dominated by typical sedge meadow species such as *Carex stricta, Aster puniceus, Thelypteris palustris, Pycnanthemum virginianum*, and *Solidago altissima* that require rich, moderately wet soils (Table 2). Only three rare Iowa fen plants (*Cypripedium parviflorum, Ophioglossum vulgatum, Viola pallens*) reach modal frequencies in this cluster (Table 3).

Cluster D (169 quadrats) is located to the lower right of Cluster C (Fig. 2). This cluster demarcates the most commonly encountered vegetation of Iowa fen mats, and is dominated by *Aster puniceus, Lycopus americanus, Muhlenbergia glomerata, Viola nephrophylla* and *Lysimachia quadriflora* (Table 2). *Carex* species are present but do not dominate, with the flora representing a wide mix of relatively low-statured forbs and graminoids. Nine rare Iowa fen plants reach modal frequencies in this cluster (Table 3) including such characteristic Midwestern USA fen taxa as *Betula pumila, Carex prairea, Cypripedium candidum, Salix candida, Solidago riddellii* and *Valeriana edulis*.

Cluster E (64 quadrats) is located in the centre-right of the ordination diagram (Fig. 2) and is dominated by species requiring both relatively high moisture levels and calcareous conditions such as *Muhlenbergia glomerata, Parnassia glauca, Eleocharis elliptica, Rhynchospora capillacea,* and *Lobelia kalmii* (Table 2). In cluster E 24 rare Iowa fen plants reach their modal frequencies in this cluster (Table 3) including *Carex sterilis, Eleocharis pauciflora, Juncus alpinus, Platanthera hyperborea, Rhynchospora capillacea, Scleria triglomerata, Spiranthes romanzoffiana, Triglochin maritimum, T. palustre* and *Utricularia minor*.

Table 2. Most frequent taxa (*n* = 20 or 21) in each of the five compositional clusters.

Cluster A (*n* = 100 quadrats)		Cluster B (*n* = 88)		Cluster C (*n* = 85)		Cluster D (*n* = 169)		Cluster E (*n* = 64)	
Species	Freq.	Species	Freq.	Species	Freq.	Species	Freq.	Species	Freq.
Campanula aparinoides	64.00%	*Thelypteris palustris*	93.18%	*Carex stricta*	82.35%	*Aster puniceus*	90.30%	*Muhlenbergia glomerata*	87.50%
Impatiens capensis	64.00%	*Impatiens capensis*	63.64%	*Aster puniceus*	82.35%	*Lycopus americanus*	88.48%	*Viola nephrophylla*	54.69%
Aster puniceus	61.00%	*Polygonum sagittatum*	61.36%	*Thelypteris palustris*	80.00%	*Muhlenbergia glomerata*	81.82%	*Lycopus americanus*	51.56%
Carex prairea	59.00%	*Aster puniceus*	50.00%	*Pycnanthemum virginianum*	51.77%	*Viola nephrophylla*	78.79%	*Parnassia glauca*	48.44%
Lycopus americanus	48.00%	*Onoclea sensibilis*	48.86%	*Solidago altissima*	50.59%	*Lysimachia quadriflora*	72.73%	*Carex prairea*	45.31%
Carex stricta	41.00%	*Triadenum fraseri*	44.32%	*Lycopus americanus*	45.88%	*Carex prairea*	66.67%	*Eleocharis elliptica*	42.19%
Pilea fontana	40.00%	*Carex stricta*	43.18%	*Campanula aparinoides*	41.18%	*Carex stricta*	63.64%	*Lysimachia quadriflora*	39.06%
Muhlenbergia glomerata	39.00%	*Campanula aparinoides*	42.05%	*Aster umbellatus*	36.47%	*Pycnanthemum virginianum*	60.61%	*Scirpus validus*	35.94%
Caltha palustris	34.00%	*Eupatorium maculatum*	31.82%	*Viola nephrophylla*	35.29%	*Carex interior*	44.24%	*Carex interior*	32.81%
Eupatorium maculatum	32.00%	*Typha latifolia*	31.82%	*Helianthus grosseserratus*	34.12%	*Campanula aparinoides*	40.00%	*Rhynchospora capillacea*	32.81%
Lysimachia thyrsiflora	25.00%	*Lycopus americanus*	26.14%	*Onoclea sensibilis*	29.41%	*Thelypteris palustris*	38.18%	*Eupatorium perfoliatum*	31.25%
Cardamine bulbosa	24.00%	*Scutellaria galericulata*	23.86%	*Muhlenbergia glomerata*	23.53%	*Eleocharis elliptica*	35.15%	*Lobelia kalmii*	29.69%
Equisetum fluviatile	24.00%	*Pilea fontana*	21.59%	*Polygonum sagittatum*	22.35%	*Eupatorium maculatum*	34.55%	*Eupatorium maculatum*	28.12%
Viola nephrophylla	23.00%	*Boehmeria cylindrica*	21.59%	*Eupatorium maculatum*	18.82%	*Lythrum alatum*	30.91%	*Carex hystericina*	28.12%
Galium labradoricum	21.00%	Immature *Muhlenbergia*	20.45%	*Fragaria virginica*	17.65%	*Salix candida*	27.88%	*Aster umbellatus*	26.56%
Thelypteris palustris	19.00%	*Carex lacustris*	18.18%	*Geum aleppicum*	17.65%	*Lobelia siphilitica*	26.06%	*Carex stricta*	26.56%
Epilobium leptophyllum	19.00%	*Aster umbellatus*	15.91%	*Polemonium reptans*	16.47%	*Sphenopholis intermedia*	24.24%	*Juncus nodosus*	26.56%
Leerzia oryzoides	19.00%	*Carex lanuginosa*	12.50%	*Poa pratensis*	15.29%	*Aster umbellatus*	20.61%	*Glyceria striata*	25.00%
Typha latifolia	18.00%	*Bidens coronata*	12.50%	*Saxifraga pensylvanica*	15.29%	*Caltha palustris*	19.39%	*Scirpus americana*	23.44%
Sphenopholis intermedia	17.00%	*Leerzia oryzoides*	12.50%	*Carex interior*	14.12%	*Parnassia glauca*	19.39%	*Equisetum arvense*	20.31%
Polygonum sagittatum	17.00%			*Caltha palustris*	14.12%			*Scleria verticillata*	20.31%

Table 3. Rare taxa (as listed in Nekola 1994) reaching modal frequencies in each compositional cluster.

Cluster A
Angelica atropurpurea
Aster junciformis
Berula erecta
Carex rostrata
Cirsium muticum
Eleocharis smallii
Equisetum fluviatile
Galium labradoricum
Menyanthes trifoliata
Mimulus glabratus
Rumex orbiculatus
Salix pedicellaris
Solidago uliginosa

Cluster B
Drosera rotundifolia
Potentilla palustris
Rubus pubescens
Sphagnum spp.
Triadenum fraseri

Cluster C
Cypripedium parviflorum
Ophioglossum vulgatum
Viola pallens

Cluster D
Betula pumila
Bromus ciliatus
Carex prairea
Cypripedium candidum
Salix candida
Salix × rubella
Salix × clarkei
Solidago riddellii
Valeriana edulis

Cluster E
Carex granularis
Carex sartwellii
Carex tetanica
Carex sterilis
Chara spp.
Eleocharis elliptica
Eleocharis pauciflora
Eriophorum angustifolium
Gentiana crinita
Gentiana procera
Gerardia paupercula
Juncus alpinus
Juncus balticus
Liparis loeselii
Lobelia kalmii
Muhlenbergia glomerata
Parnassia glauca
Platanthera hyperborea
Rhynchospora capillacea
Scleria verticillata
Spiranthes romanzoffiana
Triglochin maritimum
Triglochin palustre
Utricularia minor

Analysis of environmental co-variables

All environmental variables except K (p = 0.060) and Average Summer Precipitation (p = 0.067) demonstrated significant correlation with the ordination diagram. Maximum r^2 values for significant variables ranged from 0.0246-0.3204. For those varying within sites, pH, -10 cm soil temperature, Mg, Ca, surface soil temperature, and S were most positively correlated with Axis 1 scores, while vegetation height and P were negatively correlated (Fig. 4). N, disturbance level, % organic matter, and hummock height were positively correlated with Axis 2 scores, while soil moisture was negatively correlated. Of the factors varying only between sites, site perimeter/area ratio was positively correlated with Axis 1 scores, while site area, air temperature, and site perimeter were negatively correlated. E-W coordinate location was positively correlated with Axis 1 but negatively correlated with Axis 2 scores, while precipitation, growing season,

Table 4. Contingency table analysis showing the number of quadrats within each of the five compositional clusters represented in each of the geologic fen types. Log-linear test statistic represents significance across entire table.

Cluster	Geologic fen type				
	Till	Bedrock	Fluvial	Basin	Eolian
A	41	10	4	37	8
B	40	0	0	37	11
C	62	2	0	5	16
D	144	21	2	1	1
E	51	7	5	0	1
Significance within each geologic type					
	< 0.00005	0.0017	0.2552	< 0.00005	0.0087

Log-linear model test statistic = 221.03; df = 16; $p < 0.0000005$.

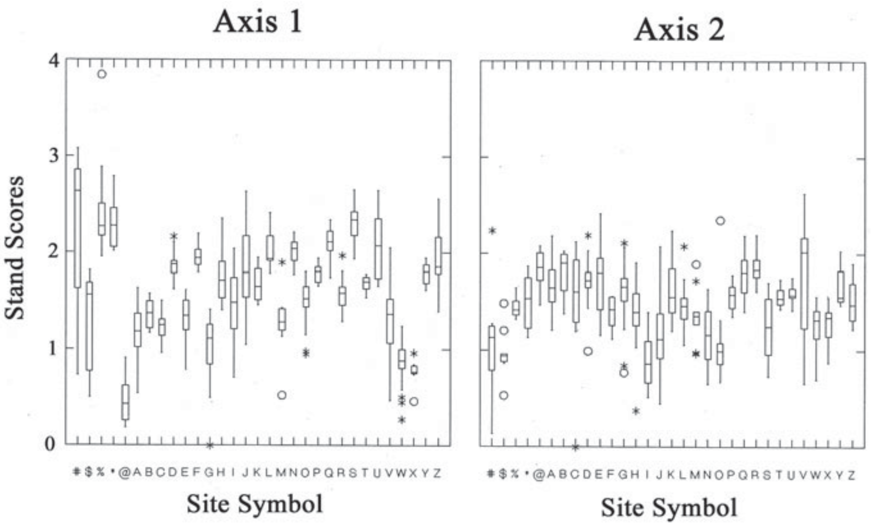

Fig. 3. Box plot of variation within each site along NMDS Axes 1 and 2. Site letter codes correspond to those in Table 1.

and N-S coordinate location were negatively correlated with Axis 1 but positively correlated with Axis 2.

The frequency of the five compositional clusters was found to significantly ($p < 0.0000005$) vary between the five geologic groups (Table 4). Glacial till sites were over-represented in Cluster D and under-represented in Clusters A and B ($p < 0.00005$). Bedrock outcrop sites were over-represented in Cluster D and underrepresented in Clusters B and C ($p = 0.0017$). Basin sites were over-represented in Clusters A and B and underrepresented in Clusters C, D, and E ($p < 0.00005$). Eolian Sand sites were over-represented in Clusters B and C and underrepresented in Clusters D and E ($p = 0.0087$). No significant patterns ($p = 0.2552$) were noted from the lone Fluvial Sand site sampled.

Discussion

Major compositional gradients

These analyses demonstrate two strong compositional gradients (3 and 2 half-change units) within Iowa fens. The principal axis varies from vegetation supporting few to many calciphiles, while the second axis varies from vegetation supporting few to many hydrophiles. The compositional clusters created to help interpret these patterns are not separated in ordination space, with quadrats from different clusters often being more similar to each other than they are to other quadrats within their own group.

The variation along Axis 1 is consistent with the

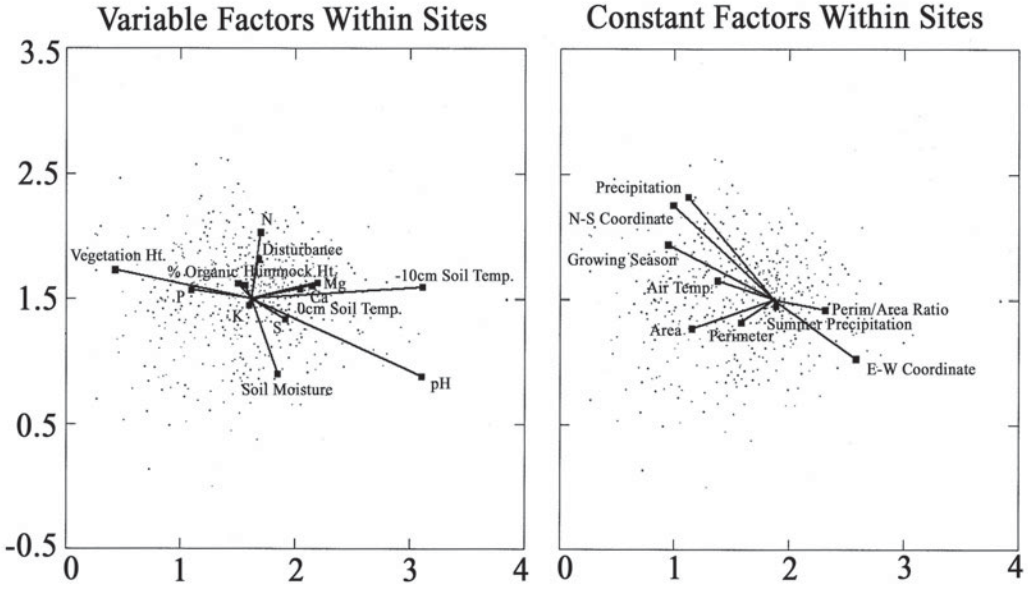

Fig. 4. Environmental variable biplots for the ordination diagram.

rich-poor fen gradient noted in most peatland landscapes, including Estonia (Masing 1982), Poland (Wassen et al. 1990a), the eastern Carpathians (Hájek 2002), Switzerland (Bergamini 2001), the southern Alps (Gerdol 1990), northwestern Europe (Sjörs 1952; Økland 1990; Sjörs & Gunnarsson 2002), Scotland (Charman 1993), boreal Canada (Vitt & Chee 1990), the northern USA (Glaser 1987; Glaser et al. 1981), northeastern USA (Motzkin 1994), and New Zealand (McQueen & Wilson 2000). Similarly, the wet-mesic gradient demonstrated along the Axis 2 has been previously documented from Illinois (Bowles et al. 1996), northern Minnesota (Glaser et al. 1990), Ohio (Stewart 1987), New York (Bernard et al. 1983), Scotland (Charman 1993), and Norway (Singsaas 1989) fens.

From a conservation perspective, the most important microsites for rare plants were those that had the highest soil moisture levels. Fourteen rare Iowa plants reached their modal frequencies in Cluster A (moderate pH and cation levels), while 25 rare species reached modal frequencies in Cluster E (high pH and cation levels). This pattern is consistent with previous investigations of Minnesota (Almendinger & Leete 1998a) and Suffolk, England (Fojt & Harding 1995) fens that have documented a positive correlation between soil water levels and rare plant richness.

Environmental co-variables

As for many other fen systems (e.g. Gerdol 1990; Vitt & Chee 1990; Wassen et al. 1990a; Charman 1993; Motzkin 1994; Fojt & Harding 1995; McQueen & Wilson 2000; Bergamini et al. 2001; Sjörs & Gunnarsson 2002) the principal axis of compositional variation was significantly correlated with pH, Ca, and Mg. The strong correlation of the principal axis with P, vegetation height, and soil temperature is likely due to the limited solubility of P compounds in areas with high soil/water pH and Ca (Bedford et al. 1999). This causes reduced primary production, fertility, and plant height in Minnesota (Almendinger & Leete 1998a), English (Boyer & Wheeler 1989), Italian alpine (Gerdol 1990) and Dutch (Verhoeven et al. 1990) fens. With increased penetration of solar energy to the ground, areas with less vegetation growth will also have higher soil temperatures. As low vegetation mats support the highest plant diversity and number of rare species in Iowa (twice the number of rare species occur in Cluster E vs. A) and other fen systems (Johnson & Leopold 1994; Wheeler & Shaw 1991; Jensen & Meyer 2001), maintenance of low available P levels will be important to fen conservation.

Previous research has also documented that soil moisture, N concentration, and disturbance level will influence fen vegetation. Water levels are one of the most commonly documented correlates with peatland vegetation gradients (Bernard et al. 1983; Stewart 1987; Økland 1989; Singsaas 1989; Glaser et al. 1990; Wassen et al. 1990a; Charman 1993; Bowles et al. 1996). Soil N has been shown to impact vegetation composition in Swiss montane (Bergamini et al. 2001) and Icelandic (Magnússon & Magnússon 1990) fens. Disturbance gradients also underlie some peatland vegetation patterns, with grazing being more intense on drier soils (Bowles et al. 1996). In Iceland these environmental factors are linked as fen sites subjected to higher grazing pressures also exhibit the highest soil N concentrations (Magnússon & Magnússon 1990).

Climate and geology may also significantly impact peatland ecology as increased precipitation and temperature lead to increased leaching rates and decreased soil Ca levels in boreal North America (Glaser 1992), Fennoscandia (Økland 1989), and Minnesota (Almendinger & Leete 1998a) fens. Similarly, in Iowa the frequency of calcareous microsites increase towards the northwest where precipitation and temperature are the lowest. A linkage between fen soil and aquifer chemistry has been previously demonstrated in Minnesota (Almendinger & Leete 1998b). Not surprisingly, Iowa sites originating from the most base-rich aquifers (e.g. bedrock, till) supported the richest fen vegetation. However, the linkage between site configuration (area, perimiter/area ratio) and vegetation has not been previously documented. While these could be related to edge-effects, they are more likely related to differential landscape positions for large (basins) vs. small (sideslope) sites, increasing the contribution of cation-rich groundwater in the latter.

Within- vs. between-site compositional gradients

While most individual sites capture between 25-50% of total observed compositional variation, this overlap was less evident along Axis 1 as compared to Axis 2. This result is to be expected as Axis 1 environmental co-variables are most strongly related to soil pH, Ca, Mg, and P, which will vary most between sites due to differences in aquifer chemistry (Almendinger & Leete 1998b), while Axis 2 scores are most strongly related to differences in soil water levels, which are largely repeated from the dry margins (lags) to wet centres of each site (Wassen et al. 1990b; Wassen & Barendregt 1992; Gerdol 1993). Thus, water levels vary more within vs. between New York fens (Slack 1994), while in nutrient levels vary more between vs. within Dutch fens (Verhoeven et al. 1990).

This differential within- and between-site variation along both axes has important consequences to the study and conservation of Iowa fens. To observe (and protect) the principal compositional gradient from poor-rich sites, multiple locations within the landscape must be considered. When only single sites are investigated or conserved, gradients associated with water levels gain importance. It is thus not surprising that as previous quantitative vegetation analysis of Midwestern fens have been limited to single or few sites (e.g. van der Valk 1975; Stewart 1987; Wilcox et al. 1986; Stoynoff 1993; McCormac & Schneider 1994; Bowles et al. 1996; Choesin & Boerner 2000) the poor-rich fen gradient has not been previously reported from this landscape. However, these single-site studies have generally documented the importance of water levels in determining vegetation pattern. Conservation prioritization simply based upon the number of rare species per site will likely lead to an over-representation of calcareous sites, as these areas support the greatest number of rare species. The rare species characteristic of poor and intermediate fens, though fewer in number, may thus be overlooked.

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