Gradient Models, Gradient Analysis, and Hierarchical Structure in Plant Communities

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Two general models of plant community structure, the community-unit and the continuum, have dominated the thinking of American community ecologists. Hypotheses derived from these and other models of plant community structure rarely have been tested, however. Traditionally, analyses of gradient structure have focused primarily on whether or not the boundaries of species response curves are clustered, which does not provide a complete picture of gradient structure. In this study, we statistically analyzed three characteristics of plant community structure along gradients (1) pattern of boundaries of species distributions, (2) pattern of modes of species response curves, and (3) whether or not species distributions exhibit hierarchical structure. In combination, these characteristics yield eight different models of vegetation structure along gradients. To determine if vegetation corresponds to any of these models, we sampled species composition using belt transects of contiguous quadrats in a total of 42 wetland sites in Minnesota and the southern Great Plains, USA. Boundaries of species distributions were clustered in 10 of 42 cases, modes of species response curves were clustered in 19 of 42 cases, and species distributions exhibited hierarchical structure in all 42 cases. Results varied between sites. Overall, four models of community structure were supported. None of the sites sampled supported the models often associated with the continuum or the community-unit. These results confirmed the need to explore alternative models of gradient structure, and suggested that more than one model of vegetation structure may be needed to represent community structure along gradients.

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Two general qualitative models, the community-unit (Clements 1905, 1936) and the individualistic concept (Gleason 1917, 1926, 1939), represent the basic conceptual framework for gradient studies in plant community ecology. Proponents of these models engaged in an acrimonious debate during the first half of this century which polarized the views of many plant ecologists (McIntosh 1985). Based primarily on multivariate analyses, the individualistic concept of species, and its modern counterpart the continuum concept of vegetation (McIntosh 1967, Whittaker 1967) is now widely accepted (McIntosh 1967, Austin 1985), yet aspects of the debate continue to intrigue both plant (Scott 1974, Westman 1983, Minchin 1989, Økland 1992, Auerbach and Shmida 1993) and animal ecologists (Richardson 1980, McIntosh 1995). To some extent, both models are nebulous (Collins et al. 1993), and explicit tests of these models are rare (Keddy 1987). Given that the individualistic and community-unit concepts were never quantitatively defined by their original proponents, perhaps it is best to redirect focus by treating these concepts for what they are, general organizational frameworks. Such
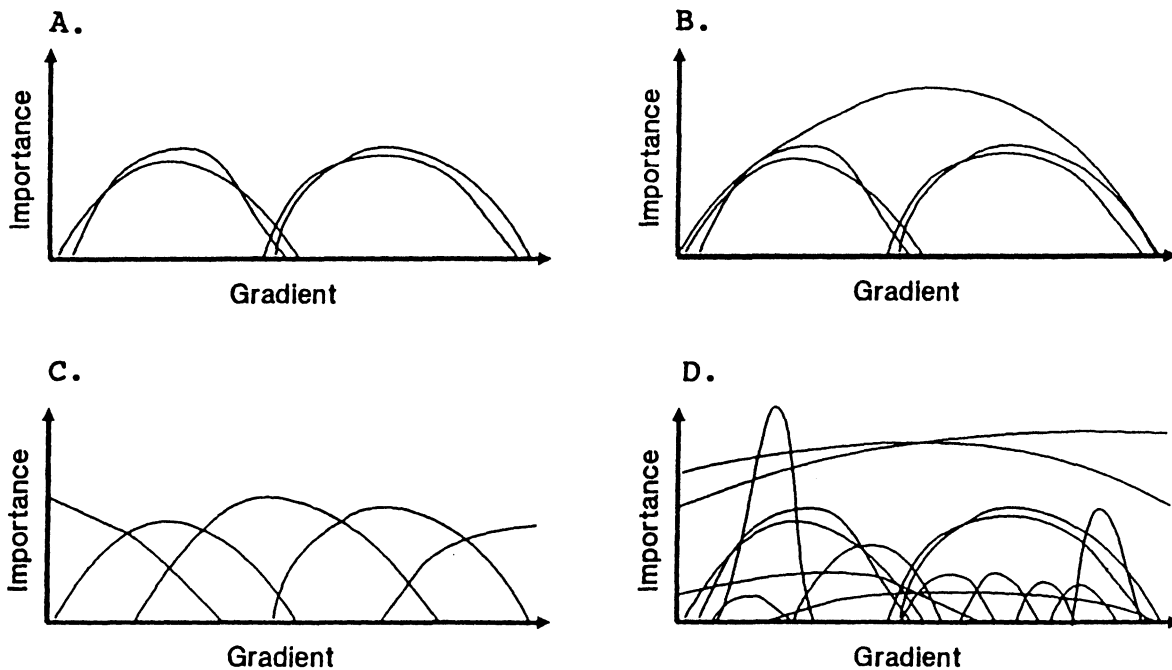
A.

B.

C.

D.

Fig. 1. Graphical presentation of four hypotheses of plant community structure along an environmental gradient: A) community-unit, B) hierarchical community-unit, C) continuum concept, and D) hierarchical continuum. Curves represent the relative abundance of a species along an environmental gradient.

an approach would allow development and measurement of meaningful quantitative characteristics of vegetation structure along gradients within these general conceptual frameworks. In this study, we focus on three independent, quantifiable measures of gradient structure: (1) pattern of boundaries of species distributions, (2) pattern of modes of species response curves, and (3) whether or not species distributions exhibit hierarchical structure. These characteristics represent the potential outcome of different mechanisms producing vegetation structure along gradients (Collins et al. unpubl.). We then measured these characteristics along gradients in wetland vegetation. Our goal was to conduct an objective and quantitative analysis of these characteristics in an effort to develop a more detailed understanding of community structure along environmental gradients.

Characteristics of community structure

The highly deterministic community-unit model of Clements (1916, 1936) has been interpreted by some to imply that plant communities are comprised of distinguishable associations of species with little overlap in species distributions among associations. Graphically, this model has been portrayed as a series of species response curves in which the starting and ending points of species distributions are clustered (Fig. 1A; Whittaker 1975, Shipley and Keddy 1987). Because of this interpre-

tation, boundaries of species response curves have been the primary focus of previous analyses of gradient structure (Underwood 1978, Dale 1984, Johnson et al. 1987, Shipley and Keddy 1987, Auerbach and Shmida 1993, Wilson 1994). Whether or not Clements envisioned vegetation to be this highly structured is uncertain; however, the modern interpretation of the community-unit represents a potential model of community structure with characteristics that can be quantified in the field. In addition to boundary clustering, however, this model also predicts that the modes of species response curves within an association are clustered.

Other interpretations of the community-unit model are possible, however (Collins et al. 1993). For example, Clements (1936) described the occurrence of "per-dominants", species that were dominant and spanned one or more association. Such a pattern would yield an alternative model (Collins et al. 1993), the hierarchical community-unit (Fig. 1B), in which boundaries and modes of species response curves are clustered, yet community structure would be hierarchical (e.g., Patterson and Brown 1991) because some species response curves would be nested within the curves of other, more dominant species.

Gleason (1917, 1926, 1939) challenged Clements' original model and suggested an alternative model in which species were distributed independently along environmental gradients. Associations of species in communities resulted from the chance interaction of

Table 1. Models of species distribution along gradients based on distribution of boundaries of species response curves, modes of species response curves, and degree of nestedness of species distributions. In addition, the number of sites that supported a particular model based on data collected from 22 transects in wetlands in the Lake Itasca State Park region of north-central Minnesota and 20 transects in playa basins in the Southern High Plains of Texas, Colorado and Oklahoma.

	Boundaries clustered	Modes clustered	Distributions nested	Playas	Lake Itasca
Hierarchical community-unit	Yes	Yes	Yes	1	1
Alternative model 1	Yes	No	Yes	2	5
Community-unit	Yes	Yes	No	0	0
Alternative model 2	Yes	No	No	0	0
Alternative model 3	No	Yes	Yes	11	5
Hierarchical continuum	No	No	Yes	6	10
Alternative model 4	No	Yes	No	0	0
Continuum	No	No	No	0	0

stochastic forces (i.e., dispersal) and deterministic forces (i.e., interspecific interactions) within a continuously varying environmental context. As noted by McIntosh (1985), the individualistic concept has been inappropriately interpreted by some to represent a random or null model of vegetation structure. The individualistic distribution of species (Gleason 1926) led to the continuum concept of vegetation (Curtis and McIntosh 1951, Whittaker 1956, 1960). The continuum is generally portrayed as a series of broadly overlapping species response curves with randomly distributed starting and stopping boundaries, and modes along an environmental gradient (Fig. 1C).

Hierarchical modifications of the continuum have been described implicitly by Gauch and Whittaker (1972) and explicitly by Collins et al. (1993). Gauch and Whittaker (1972) proposed that modes of dominant species were regularly spaced and encompassed several curves of subordinate species. The model by Collins et al. (1993) is derived from Kolasa's (1989) hierarchical model of community structure, the continuum concept, and the core-satellite species hypothesis (Hanski 1982, Hanski and Gyllenberg 1993). Kolasa's model predicts hierarchical structure because species with narrow niches are restricted in distribution and occur as nested subsets within the habitat of broadly distributed, dominant species. These widely distributed dominant species are analogous to "core" species in Hanski's (1982) model, whereas narrowly distributed species correspond to "satellite" species in the model. Within a gradient context (e.g., Collins et al. 1993), the hierarchical continuum model predicts that modes and boundaries of species response curves are random, but because distributions are hierarchical, this model predicts that species distributions are nested (Fig. 1D).

Explicit tests of hypotheses derived from the continuum, the community-unit, or any other gradient model are rare in vegetation science (Keddy 1987). Indeed, the discipline has been criticized for want of a rigorous scientific approach, particularly a lack of hypothesis testing as a mechanism for accepting or rejecting concepts and models (Keddy 1987, Wilson 1991, Gurevitch

and Collins 1994). Shipley and Keddy (1987) attempted to overcome this deficiency by testing predictions regarding boundary clustering based on the continuum and community-unit models of vegetation structure. But the degree of boundary clustering is only one quantifiable variable that can be derived from these models. As noted above, other quantitative variables include the distribution of modes of species response curves along the gradient, and whether or not species distributions exhibit hierarchical structure. Based on these three attributes, there are eight alternative models of community structure, of which only four have been, more or less, previously described (Table 1). None of these characteristics (boundary clustering, clustering of modes, nestedness) alone is sufficient to discriminate among models, but taken together with appropriate indices to measure each characteristic, a more accurate assessment of community structure along gradients can be determined.

In this study, we analyzed patterns of boundary clustering, clustering of modes, and nestedness of species response curves along 42 wetland gradients to determine if vegetation structure conforms to predictions derived from any of the eight alternative models of vegetation structure in Table 1. Admittedly, this analysis is descriptive in that it reflects a search for pattern, yet we argue that pattern must be determined before detailed analyses of processes and mechanisms can be performed. We believe our approach is rigorous, however, because we statistically analyzed patterns in field data in comparison to patterns derived from different models of community structure.

Methods and materials

Study areas

Shoreline wetland communities were chosen as study sites because of strong gradients produced by varying degrees of soil moisture and nutrients, and diverse assemblages of plant species (Sculthorpe 1967, Armstrong 1975, Spence 1982, Mitsch and Gosselink 1986).

In addition, wetlands have served as model systems in previous studies of gradient structure (Shipley and Keddy 1987, Økland 1992). Study sites were selected in two physiognomically distinct wetland systems: emergent wetlands in lakes and ponds in Itasca State Park, Minnesota, USA, and playa lake basins in the Southern High Plains of Texas, Oklahoma, and New Mexico, USA.

Field methods

At each site, contiguous 25-cm by 50-cm quadrats were located along belt transects with the long axis of each quadrat oriented perpendicular to the wetland gradient. The length of transects, and thus the number of quadrats, varied in relation to the radius of a site. At Itasca, transects ($n = 22$) varied in length from 50 to 150 quadrats (12.5 to 50 m). These transects originated at the edge of emergent wetland vegetation and terminated 20 quadrats into the upland forest community. Playa transects ($n = 20$) ranged in length from 50 to 220 quadrats (12.2 to 54 m). Transects originated at the center of the playa and extended through the basin floor vegetation and into the adjacent shortgrass prairie. Aerial cover of each species was visually estimated (Wilson and Lee 1994) in five percent cover classes in each quadrat.

Data analysis

To evaluate degree of boundary clustering of species response curves, the number of starting and stopping boundaries was calculated per quadrat. As with previous studies of boundary clustering (Pielou 1977a, Underwood 1978, Dale 1984, Shipley and Keddy 1987, Auerbach and Shmida 1993), we assumed that breaks in species distribution did not necessarily mean that the species was physiologically unable to occur in these intervals at each site. Therefore, only the initial lower and upper boundaries of species distributions were used for this analysis. Morisita's index (Hurlbert 1990) was used to determine whether or not species boundaries were clustered:

$$I = Q \sum_{i=1}^{Q} \left(\frac{n_1}{N} \right) \left(\frac{n_i - 1}{N - 1} \right)$$

where Q is the number of quadrats, n_i is the number of starting and stopping boundaries in the ith quadrat, and n is the total number of boundaries. Calculations did not include the first and last quadrats of a transect. If $I = 1$, boundaries are random, if $I < 1$ boundaries are regularly dispersed, and if $I > 1$ boundaries are clus-

tered. A chi-square test was used to determine significance.

Modes of species response curves along a transect were considered to occur in the quadrat with the highest cover value. Degree of aggregation (P) of species modes was determined using the index of Poole and Rathcke (1979) which calculates the sample variance of distance between modes:

$$P = \frac{\sum_{i=0}^{k} \{y_{i+1} - y_i - [1/(k+1)]\}^2}{k + 1}$$

where k is the number of species, $y_{i+1} - y_i$ is the distance between modes, and $1/(k+1)$ is the mean of $y_{i+1} - y_i$. If $P = 1$, modes are randomly distributed, if $P < 1$ modes are regularly distributed, if $P > 1$ modes are aggregated. Using this index, we can test the null hypothesis that species modes are randomly distributed along an environmental gradient using the chi square distribution (Poole and Rathcke 1979).

Hierarchical structure was determined by calculating the degree of nestedness in species distributions (Patterson and Brown 1991) along each transect using the nestedness index of Wright and Reeves (1992):

$$N_c = \sum_{i=1}^{K-1} \sum_{m=i-1}^{K} \sum_{j=1}^{S} X_{ij} X_{mj}$$

where S is the total number of species, K is the number of quadrats, and $X_{ij} = 1$ if species j is present at quadrat I and 0 if it is absent. The nestedness index, N_c, counts the number of times that a species' presence in a quadrat correctly predicts that species' presence in quadrats that are more species-rich (Wright and Reeves 1992).

The value of N_c is then used to calculate the relative nestedness index (C) which ranges from 0 for complete independence of species distributions to 1 for perfect nestedness:

$$C = \frac{N_c - E\{N_c\}}{\max \{N_c\} - E\{N_c\}}$$

where $E\{N_c\}$ is the expected value and $\max \{N_c\}$ is the value of N_c for a perfectly nested matrix. Cochran's Q, considered a more conservative test than z-scores (Wright and Reeves 1992), was used to test for significance of nested species distributions.

Spearman's rank correlation coefficients were calculated for Itasca and playa data sets to determine if any of the three indices of gradient structure were correlated with either transect length or total species richness.

Table 2. Indices of community structure for wetland gradients at Lake Itasca State Park, Minnesota. Columns represent, respectively, index values for boundary clustering, nestedness and distribution of modes. The yes/no responses signify whether or not values were significant at each site. Habitat types are designated as [L] for lacustrine shoreline and [S] sedge mat.

Site name	No. of plots	No. of species	Boundaries clustered	Modes clustered	Distributions nested	Model supported
Bear Paw Point[S]	100	32	1.27 NO	0.72 NO	0.20 YES	HC
Beaver Lake[L]	68	19	1.72 NO	0.47 NO	0.01 YES	HC
Bog D[S]	129	47	2.04 YES	4.40 NO	0.14 YES	Alt. 1
Bog F[S]	90	35	2.66 NO	2.72 NO	0.35 YES	HC
Bohall 1[S]	80	25	1.79 YES	1.12 NO	0.22 YES	Alt 1
Bohall 2[S]	120	32	1.84 NO	0.78 NO	0.25 YES	HC
Bohall 3[S]	100	34	2.52 NO	2.33 YES	0.29 YES	Alt. 3
DeSoto Trail, North[L]	145	17	2.52 NO	0.38 NO	0.15 YES	HC
DeSoto Trail, East[L]	75	9	2.92 NO	1.43 NO	0.30 YES	HC
DeSoto Trail, South[L]	80	14	2.97 YES	0.70 NO	0.29 YES	Alt. 1
DeSoto Trail, West[L]	62	13	1.80 NO	0.61 NO	0.16 YES	HC
Floating Bog Bay 1[S]	110	40	1.54 YES	1.36 NO	0.16 YES	Alt. 1
Floating Bog Bay 2[S]	87	39	1.59 NO	1.50 YES	0.14 YES	Alt. 3
French Creek 1[S]	85	35	3.0 YES	2.34 YES	0.34 YES	HCU
French Creek 2[S]	90	36	2.74 NO	1.76 YES	0.32 YES	Alt. 3
Little Mantrap Lake[L]	90	28	2.14 NO	0.87 NO	0.14 YES	HC
Midpoint Bog[S]	100	42	2.72 YES	1.38 NO	0.20 YES	Alt. 1
Schoolcraft Island[L]	65	65	2.66 NO	3.37 YES	0.25 YES	Alt. 3
Scott's Favorite Lake, South[L]	50	17	1.91 NO	0.49 NO	0.19 YES	HC
Scott's Favorite Lake, West[L]	50	16	1.62 NO	1.10 NO	0.19 YES	HC
Tamarack Lake[S]	100	33	3.05 YES	1.46 YES	0.26 YES	HCU
Tamarack Point[S]	85	33	1.85 NO	1.92 YES	0.37 YES	Alt. 3

Results

Itasca wetlands

Wetlands at Itasca often had abrupt transitions between open water and sedge mat surfaces. The lakeward portion of sedge mats was often dominated by *Carex comosa* F. Boott. and *Calla palustris* L. Several other *Carex* spp. occurred within the sedge mats. Moats were common at the sedgemat–upland interfaces. Lacustrine shorelines were dominated by *Sagittaria rigida* Pursh. adjacent to a narrow zone of *Calamagrostis stricta* (Timm.) Koel. A broad zone of several *Carex* spp. extended from the *C. inexpansa* zone to the uplands.

Indices of boundary clustering and distribution of modes were variable among transects at Itasca (Table 2). Boundaries of species response curves were significantly aggregated at 15 of 22 sites. Modes of species response curves were significantly aggregated at seven of 22 sites. Species distributions were significantly nested at all 22 sites indicating hierarchical structure. Overall, community structure in Itasca wetlands was variable among sites. The hierarchical continuum was supported at 10 sites, the hierarchical community-unit was supported at two sites, and alternative models 1 and 3 were each supported at five sites (Table 1). Five wetlands at Itasca were sampled with two or more transects at different locations. In four of these five, the gradient structure, reflected by index scores, differed among transects within a single wetland.

Playa lake basins

Although the overall physiognomy of playas was variable, 18 playas had three visually identifiable vegetation zones, but only two zones were discerned in the remaining two playas. Five playas contained a central zone dominated by annual species such as *Ambrosia grayii* (A. Nels.) Shinners, *Kochia scoparia* (L.) Schrad., and *Xanthum strumarium* L. The central vegetation zone of the 15 playas remaining was dominated by *Agropyron smithii* Rydb., *Buchloë dactyloides* (Nutt.) Engelm., and *Lippia cuneifolia* (Torr.) Steud. Several species were common in the outer playa zones, including *Schedonnardus paniculata* (Nutt.) Trel., *Kochia scoparia*, *Aristida longiseta* Steud.-Reydb., and *Lippia cuneifolia*. The shortgrass prairie upland was typically dominated by *Bouteloua gracilis* (H.B.K.) Lasg. ex Griffiths and *Buchloë dactyloides*.

Values for the indices of boundary clustering and distribution of modes were variable among the playa transects (Table 3). Boundaries of species response curves were significantly aggregated at three of 20 sites. Modes of species response curves were aggregated in 12 of 20 sites. Species distributions were significantly nested at all 20 sites indicating hierarchical structure. Overall, the hierarchical continuum concept was supported at six sites, the hierarchical community-unit was supported at one site, alternative model 1 was supported at two sites, and alternative model 3 was supported at 11 sites (Table 1).

Table 3. Indices of community structure for playa lake basins in the Southern High Plains of Texas, Oklahoma and New Mexico. Columns represent, respectively, index values for boundary clustering, nestedness and distribution of modes. The yes/no responses signify whether or not values were significant at each site. Habitat types are designated as [L] for lacustrine shoreline and [S] sedge mat.

Site name	No. of plots	No. of species	Boundaries clustered	Modes clustered	Distributions nested	Model supported
Golden Lake	150	22	1.29 YES	0.84 YES	0.32 YES	HCU
Kiowa 14	40	11	0.57 NO	0.41 NO	0.37 YES	HC
Kiowa 36	80	17	2.02 YES	0.43 NO	0.30 YES	Alt. 1
Kiowa 125	120	22	0.92 NO	0.56 NO	0.29 YES	HC
Kiowa 127A	130	18	2.86 YES	0.66 NO	0.53 YES	Alt. 1
Kiowa 127B	150	26	2.09 NO	1.53 NO	0.45 YES	HC
Kiowa 128	200	18	0.78 NO	0.64 NO	0.37 YES	HC
Kiowa 129	170	24	1.44 NO	0.98 NO	0.48 YES	HC
Rita Blanca 21A	65	12	1.94 NO	0.96 YES	0.45 YES	Alt. 3
Rita Blanca 21B	80	17	1.36 NO	0.76 YES	0.28 YES	Alt. 3
Rita Blanca 21D	80	11	1.32 NO	0.70 YES	0.58 YES	Alt. 3
Rita Blanca 22A	80	24	1.55 NO	0.90 YES	0.42 YES	Alt. 3
Rita Blanca 22B	60	17	0.51 NO	0.62 YES	0.50 YES	Alt. 3
Rita Blanca 22C	70	16	1.39 NO	0.60 YES	0.47 YES	Alt. 3
Rita Blanca 22D	50	17	1.65 NO	1.21 YES	0.16 YES	Alt. 3
Rita Blanca 44	140	17	1.44 NO	19.1 YES	0.52 YES	Alt. 3
Rita Blanca 46	85	12	2.30 NO	0.68 NO	0.59 YES	HC
Rita Blanca 48	130	9	1.76 NO	0.56 YES	0.66 YES	Alt. 3
Rita Blanca 70	220	19	2.21 NO	0.87 YES	0.30 YES	Alt. 1
Rita Blanca 136	57	11	1.02 NO	0.59 YES	0.90 YES	Alt. 3

There was no correlation between transect length, species richness and the indices of boundary clustering, clustering of modes, or nestedness at either the Itasca or the playa sites.

Discussion

Plant community structure along wetland gradients supported four of the eight possible models in Table 1: the hierarchical continuum, the hierarchical community-unit, and two previously undescribed models. Nestedness was observed on all transects, significant boundary clustering was observed in 10 of 42 transects, and significant clustering of modes occurred on 19 of 42 transects. The two models with most support from the field data, the hierarchical continuum and model 3, both predict that boundaries of species response curves are random, and that species distributions along the gradient are nested. The models differ in that one predicts clustered modes, while the other predicts that modes of response curves are random.

The consistent pattern of nestedness represents a potentially important aspect of plant community structure. Indeed, a model of gradient structure proposed by Gauch and Whittaker (1972) suggests that hierarchical structure may exist, but such structure has not previously been quantified. Hierarchical structure is predictable, however, from dominance patterns in competitive hierarchies (Kolasa 1989, Kodric-Brown and Brown 1994). One assumption of many models of distribution and abundance is that dominant species are widely distributed and subordinate species are locally distributed (Hanski 1982, Brown 1984, Kolasa 1989). Although this pattern has not been explored in wetland plant communities, this relationship does exist, for example, in other types of herbaceous vegetation, such as tallgrass prairie plant communities (Collins and Glenn 1990, 1991). In tallgrass prairie, the distribution and abundance of subordinate species are regulated, to some extent, by dominant species at both small and large spatial scales (Collins et al. unpubl.). Hierarchical structure could develop simply as a consequence of dominance. Strong patterns of dominance have been noted in wetland plants (Gaudet and Keddy 1988). The ability of dominant species to modify the local environment, however, could enhance hierarchical structure. This mechanism, which was inherent in Clements' (1916) model of community succession, has been elaborated in recent theoretical discussions of community dynamics (Roberts 1987, Wilson and Agnew 1992). Wedin and Tilman (1990) have shown that dominant prairie grasses alter resource availability in the local soil environment. In wetlands, differential peat accumulation in sedge mat communities affects community structure by raising surface levels (Hogg and Wein 1988). Such changes produce reciprocal feedbacks between vegetation and environment (Hobbie et al. 1993), which may further enhance dominance and hierarchical structure.

Clustering of boundaries of species response curves often occurs at sharp environmental discontinuities (McIntosh 1967). The degree of boundary clustering varies with spatial scale (Pielou 1977b, Wilson and Lee 1994). Likewise, the extent of boundary clustering can be inconsistent among transects at the same site

(Dale 1984). In wetlands, the sedge mat vegetation often has a sharp boundary with emergent aquatic vegetation (Mitsch and Gosselink 1986). Mechanisms creating more-or-less discrete boundaries in species distributions include wave action (Keddy 1983, Weisner 1991), extent and duration of flooding (Van der Valk and Welling 1988), and "windrowing", deposition of seeds by wind at the shoreline (Penfound 1953, Van der Valk and Welling 1988). Interaction of environmental modification by dominant species and the nested distribution of subordinates can yield assemblages of species with zonation-like patterns along environmental gradients. Such a pattern could yield clustered modes, as well as boundary discontinuities. However, the importance of these mechanisms within a given wetland will vary with the size of the wetland, water level fluctuations, direction of predominant winds, etc.

The highly stochastic effects of dispersal, in conjunction with interspecific interactions and disturbance in a dynamic environmental context, will produce variable community structure at small spatial scales. Thus, it is not surprising that several models of community structure were supported in this study. Indeed, there is no need to assume that only one model of community structure will suffice to describe patterns of species distribution along environmental gradients at any spatial and temporal scale. The number of mechanisms affecting gradient structure, and the relative importance of these mechanisms, will change with the spatial and temporal scales observed (Hoekstra et al. 1991, Reed et al. 1993). For example, dispersal is one mechanism creating pattern along environmental gradients, yet the importance of dispersal will vary with scale. Along small-scale gradients, such as in the wetlands we sampled, a large number of species can reach a large proportion of the gradient which could produce the hierarchical structure observed in this study. Dispersal along elevational gradients, often used as surrogates for continental gradients (Whittaker 1956, 1960), may be a less important mechanism affecting gradient structure than large-scale climatic, edaphic, and environmental factors. These factors change at slower rates over longer time scales, thus, community structure over large regions will be less dynamic over short time periods compared to the small-scale wetland gradients studied here.

Although the continuum is widely accepted by community ecologists (Austin 1985, Minchin 1989, Austin and Gaywood 1994), none of the gradients that we analyzed supported predictions derived from traditional interpretations of the continuum concept. Shipley and Keddy (1987) found no support for the continuum in their study of wetland vegetation. Indeed, given that community structure is likely to vary with scale, the study of wetland gradients alone is not sufficient to resolve the continuum/community-unit debate, nor is it likely that such a "debate" can truly be resolved (Allen

and Hoekstra 1992). Rather, we argue for the need to develop and test alternative models of gradient structure (e.g., Austin and Smith 1989, Collins et al. 1993). Development and analysis of alternative models should focus not only on the validity of a given model, but also on the spatial and temporal domains within which the model may or may not apply (Pickett et al. 1994). Such an approach will yield greater understanding of gradient structure, and provide a pluralistic approach to understanding plant community structure at a variety of spatial and temporal scales (McIntosh 1987, Wiegleb 1989). As a consequence, vegetation science will move from a descriptive to a more predictive discipline, resulting in a stronger conceptual framework for the study of pattern and process in plant communities.

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