The hierarchical continuum concept

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Abstract. Two general models have been proposed to explain the structure of the plant community: the community-unit model of Clements and the continuum model of Whittaker and Curtis, the latter based on Gleason's individualistic distribution of species. It is generally assumed that most ecologists now accept the continuum model. Empirical evidence suggests, however, that the continuum in its current form does not fully describe the observed patterns of vegetation along environmental gradients. In this paper, we introduce the hierarchical continuum as a general concept to represent dynamic community structure along regional spatial gradients. The hierarchical continuum is derived from a combination of the individualistic distribution of species, hierarchical assemblage structure, and the core-satellite species hypothesis. The hierarchical continuum concept predicts that the distribution of species across sites in a region will be polymodal, which reflects hierarchical structure, and that the distribution and abundance of species within and between sites will be spatially and temporally dynamic. Regional distribution of plant species in North American tallgrass prairie, southeastern floodplain hardwood forests, northern upland hardwood forests, and boreal forests were either bimodal or polymodal as predicted by the hierarchical continuum concept. Species in tallgrass prairie were spatially and temporally dynamic with an average turnover of 8-9 species per 50 m^2 yr^{-1}. In addition, the hierarchical continuum concept predicts the potential for fractal (self-similar) patterns of community structure, and provides a framework for testable hypotheses concerning species distributions along environmental gradients.

Keywords: Community structure; Continuum model; Gradient analysis; Hierarchical structure.

Introduction

The structure of plant communities has been widely debated throughout much of this century (e.g. Clements 1916; Gleason 1917; Cain 1939; Goodall 1963; McIntosh 1967; Daubenmire 1966; Dansereau et al. 1968; Langford & Buell 1969). Essentially, two general models have been proposed: the community as discrete unit, and the continuum. The community-unit hypothesis formulated by Clements (1936) states that communities are highly structured repeatable and identifiable associations of species controlled by climate. Clement's model of vegetation is often depicted graphically as a series of non-overlapping groups of species response curves along an environmental gradient (Fig. 1A). However, Clements (1936) clearly pointed out that the associations within a formation are often linked by the presence of per-dominants, i.e. species that occur as dominants and subdominants throughout several associations. Thus, a more correct representation of the Clementsian scheme would show several curves of wide ranging species spanning clusters of curves representing dominants of faciations and locations (Fig. 1B).

The alternative continuum model of Whittaker (1951, 1953) and Curtis (1959) states that plant communities change gradually along complex environmental gradients, such that no distinct associations of species can be identified (Fig. 1C). Gauch & Whittaker (1972) established nine hypotheses concerning the structure of the continuum. The basis of these hypotheses was the notion that species response curves along environmental gradients are Gaussian. Empirical data, however, depict response curves to be rarely Gaussian leading some to question the structure of the continuum (e.g. Austin 1980, 1985, 1990). Indeed, species response curves are more often skewed and sometimes bimodal, rather than normal (Westman 1980; Austin 1980; Austin & Austin 1980; Minchin 1989). However, a continuum or a community-unit can exist if the species response curves are skewed, leptokurtic, bimodal, or normal.

While the continuum model grew out of Gleason's (1917, 1926, 1939) essays on the individualistic distribution of species, the individualistic hypothesis and the community continuum should not necessarily be considered synonymous (Goodall 1963). The individualistic hypothesis is a species-scale phenomenon involving the tolerance of individuals of different species to local environmental conditions, which may include interspecific competition and other interactions (McIntosh in press). In contrast, the continuum is a community-level construct of the collective distributions and abundances of species along environmental gradients. It is
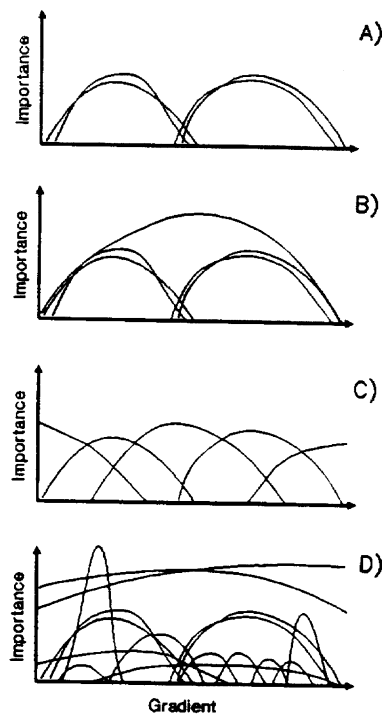
Fig. 1. Schematic models of species distribution along environmental gradients. A. Strict but questionable interpretation of Clement's model. B. Hierarchical structure in Clement's model. C. The individualistic distribution of species producing a continuum. D. The hierarchical continuum model.

possible, under the appropriate conditions, that the individualistic distribution of species could produce species associations as shown in Fig. 1A or 1B, as well as those in Fig. 1C or 1D (Roberts 1987).

Although Austin (1990) recently concluded that most ecologists now accept the continuum model to be correct, the debate concerning the validity of these models continues (Scott 1974; Westman 1983; Shipley & Keddy 1987; Minchin 1989). Westman (1983) suggested the 'great debate' endures because empirical evidence exists that supports both points of view. On the other hand, Shipley & Keddy (1987) determined that neither model applied to species distributions along complex environmental gradients in wetlands. Roberts (1987) suggested that both the community-unit and continuum models were consistent with a mechanistic view of vegetation development. From a hierarchical perspective, the two models are not competitive; rather, they reflect differences in scale of perception (Hoekstra, Allen & Flather 1991; Allen & Hoekstra 1991, 1992). It would appear that the 'great debate' has not yet been resolved.

Our general purpose in this paper is to develop a new hypothetical concept of plant community organization, the hierarchical continuum, and then to evaluate the

concept using empirical evidence from continental gradients in North American plant communities. Space limitations do not allow for full presentation of the concept, so only a brief outline of the theoretical development and some supporting data will be presented. We offer the hierarchical continuum as a source of alternative hypotheses to be tested against those derived from the community-unit and continuum models, and perhaps to help stimulate further analysis and development of new models of species distributions along gradients.

The Hierarchical Continuum concept

The hierarchical continuum has been derived from three models of species distribution among sites in a region: Gleason's (1917, 1926, 1939) individualistic hypothesis, hierarchical community structure (Kolasa 1989), and the core-satellite species hypothesis (Hanski 1982a, 1991). The individualistic hypothesis supplies the foundation for the model because it is flexible, and it provides the best framework for pluralistic vegetation science (Wiegleb 1989). The primary assumption of the models of Hanski (1982a) and Kolasa (1989) is that a positive relationship exists between the number of sites at which a species occurs and its average abundance in a region (McNaughton & Wolf 1970; Hanski 1982a; Bock & Ricklefs 1983; Brown 1984; Ricklefs 1987; Bock 1987; Kolasa 1989). This relationship is common, but not universal (Adams & Anderson 1982; Burgman 1989), and the potential bias of this relationship requires further analysis (Wright 1991). Species conforming to the model are 'core' species which are typically dominants that occupy > 90% of sites in a region. 'Satellite' species are subordinate species found at < 10% of sites in a region. Occurrence of 'urban' (locally distributed, high abundance) and 'rural' (widely distributed, low abundance) species (Hanski 1991) reduce the predictive power of the relationship between distribution and abundance (Fig. 2A). Core, satellite, urban, and rural species can be easily identified from a gradient perspective (Fig. 2B). Combining these species distributions along a gradient results in a complex community structure (Fig. 1D).

Hierarchy theory provides a mechanism for the analysis of structure (Allen & Starr 1982; O'Neill 1989; Kolasa & Pickett 1989). Any phenomenon of interest can be broken down into sub-units which may define mechanisms producing pattern at the focal level. Higher level entities provide constraints on the focal level. Hierarchies may be nested or non-nested. A nested hierarchy is one in which the highest level contains and is composed of all lower levels, such as the traditional taxonomic hierarchy (Allen & Starr 1982). Non-nested hierarchies relax this condition, but maintain the hierarchical struc-

ture of constraint from above and mechanism from below the focal level. Non-nested hierarchies provide for the possibility of collective or additive properties. For example, the continuum may be viewed as a collective property of the individualistic distribution of species. The hierarchical structure of vegetation has become increasingly recognized. For example, Mirkin (1989) suggested that relevés could be combined in a number of ways which lead him to suggest that the continuum was hierarchical. McLaughlin (1992) found that floristic areas were hierarchically structured. Another example is Acker's (1990) suggestion that vegetation is part of a non-nested hierarchy with the environment.

Kolasa's (1989) model of species regional distribution and abundance is modified here to a non-nested hierarchy based on division of an environmental template by species with different degrees of specialization. Essentially, the habitat is hierarchically heterogeneous such that the habitat template is composed of patches which can be divided into smaller patches, etc. As used here, the model is non-nested because the habitat template for different species may overlap within a level.

Species in a collection from several sites will exhibit varying degrees of specialization to habitat. Thus, species abundance patterns will reflect specialization, and the degree to which the habitat template can be fragmented (Fig. 3A). Constraints within the hierarchy may be imposed by habitat variables (climate, parent material) on broad ranging species, and in turn, the broad ranging species may impose constraints on intermediate range species, etc. For example, a two-tiered competitive hierarchy has been hypothesized for tallgrass prairies where the dominant matrix forming grasses limit the distribution and abundance of non-matrix species (e.g. Collins 1987; Glenn & Collins 1990).

Hanski (1982a) developed a stochastic model of species distribution and abundance based on dynamics of immigration and extinction. In this model, the combined distribution of all species among all sites is bimodal, from which Hanski formulated the core-satellite species hypothesis. This model predicts that species distributions will fluctuate independently between the core and satellite modes, and species with intermediate distributions will be the most dynamic. Hanski (1991) modified the core-satellite model such that some species may attain stable distributions, whereas others may fluctuate until they reach an equilibrium. Thus, the core-satellite hypothesis, derived from an individual species meta-population model, is a spatially and temporally dynamic hypothesis as is Gleason's (1926) individualistic hypothesis. Year-to-year fluctuations in abundance and distribution occur in response to well documented annual variations in environment (Wiens 1976). Patterns conforming to the core-satellite hypothesis have
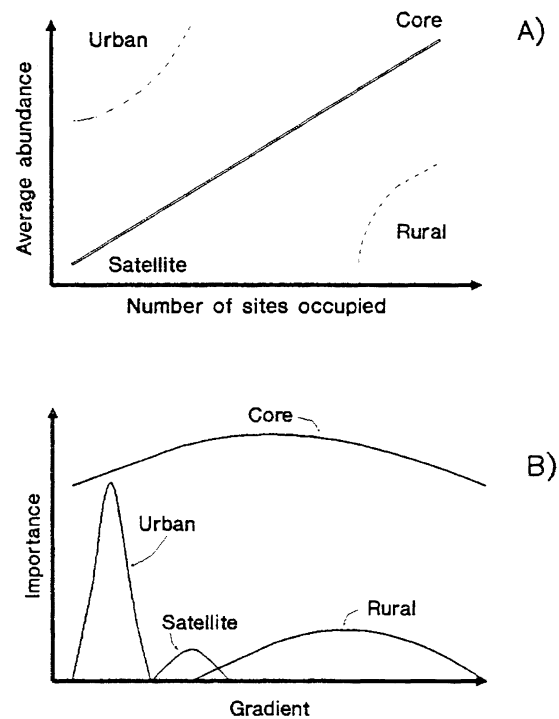

Fig. 2. A. Schematic relationship between the distribution and abundance of core, satellite, urban, and rural species. B. Distribution of core, satellite, urban, and rural species along a hypothetical gradient.

been found for some plant communities (Hanski 1982b; Gotelli & Simberloff 1987; Collins & Glenn 1990, 1991) but such patterns are less evident in animal communities (Gaston & Lawton 1989). Indeed, plant species distributions are often polymodal rather than bimodal (Collins & Glenn 1990, 1991), which yields patterns also predicted by Kolasa's model.

Combining Kolasa's hierarchical model with the core-satellite hypothesis leads to specific predictions regarding species regional distribution and abundance, and the structure of the continuum. Core species would be comparable to Kolasa's broad-ranging species at the highest hierarchical level and satellite species would include locally distributed subordinate species. If clear hierarchical breaks occur in community structure, then Kolasa's model predicts a polymodal regional pattern of distribution in which the size of the mode decreases as distribution increases (Fig. 3B). By adding the core-satellite model, the spatial and temporal patterns of species distribution become dynamic. The broad distribution of core and rural species may minimize the effects of environmental fluctuations making these species less dynamic than satellite and urban species. With regard to the continuum, these models suggest that some species will occur throughout the gradient (core spe-
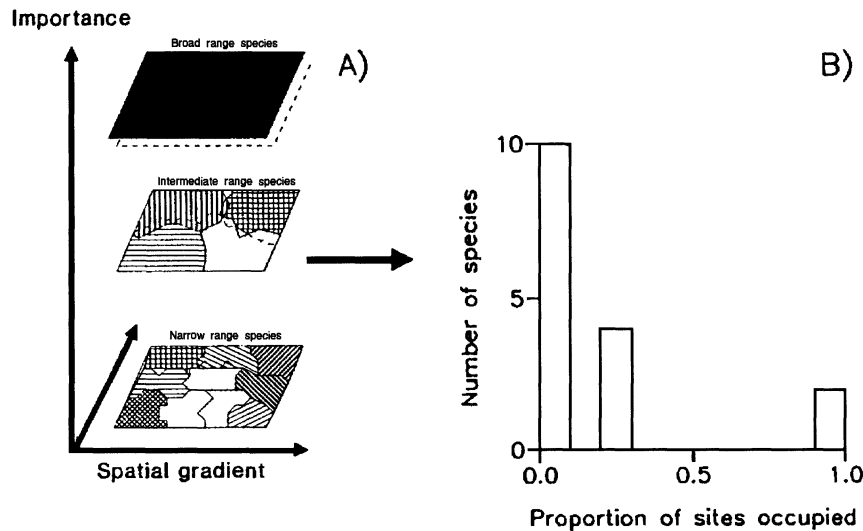
Importance

Fig. 3. A. The habitat template and hierarchical model of community structure (modified from Kolasa 1989. B. Pattern of distribution and abundance predicted by the model of hierarchical community structure.

cies), others will occupy large portions of the gradient (rural species), and many species will be locally distributed (urban and satellite species, Fig. 1D). It is these locally distributed species, however, that increase gamma and beta diversity along gradients (Whittaker 1977).

continuum, generated a pattern of species distribution that was significantly different from the four data sets (Kolmogorov- Smirnov test: $P \ll 0.05$ for each comparison). This would suggest that some continuum models do not adequately represent field data.

Testing the model

Tests of the hierarchical continuum should include (1) analysis of species distributions across sites in a region to test for polymodal distributions, and (2) repeated sampling of sites in a region to determine if species distributions and abundances are spatially and temporally dynamic. Four data sets from North American plant communities were used to determine if regional distribution patterns (i) contain core species which extend throughout the area sampled, and (ii) are polymodal as predicted by the hierarchical continuum concept. Tallgrass prairie (Diamond & Smeins 1988), southeastern floodplain hardwood forest trees (Quarterman & Keever 1962), northern upland hardwood forest herbs and trees, and boreal forest herbs and trees[1] were analyzed. For each vegetation type, there is a core group of species which occurs at >90% of the sites. This indicates that a small number of species span the compositional gradient, an aspect of gradient analysis that is often neglected. A simulated Coenocline Simulation program of Gauch & Whittaker (1972) using the parameters they list (Fig. 2C), purported to represent the

Results

Three data sets have more than two modes reflecting a weak hierarchical structure (Fig. 4A, B, C). The satellite mode in the grassland data set is shifted to the right (Fig. 4A) because Diamond & Smeins (1988) did not list species with highly restricted distributions or with low average cover values. These results suggest that there is a hierarchical pattern of species distributions within a region. Distinct breaks in the hierarchy do not occur as would be predicted from a strict interpretation of Kolasa (1989). Rather, the dominance hierarchy is fuzzy (Roberts 1989) in response to the influence of rural and urban species.

Patterns of temporal dynamics were assessed following Rahel (1990) and using long-term data from Konza Prairie, Kansas, on seven upland sites sampled annually in permanently located quadrats from 1981 or 1983 until 1990 (Collins & Glenn 1991). The persistence of an assemblage can be measured at three numerical scales which form a nested hierarchy. At the finest scale, the persistence of absolute species abundances can be determined. Variability of absolute abundances was determined by calculating the coefficient of variation (CV) for the abundance of each species over time at each site. Abundance was measured as average cover of each species in 20 10-m^2 quadrats within each site. The average of the CV's is a measure

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[1]The last two data sets are from the Wisconsin Plant Ecology Laboratory, and are part of the data used by Curtis (1959). These data are available from Dr. Charles E. Umbanhower, Dept. Biology, St. Olafs College, Northfield, MN 55057, USA.
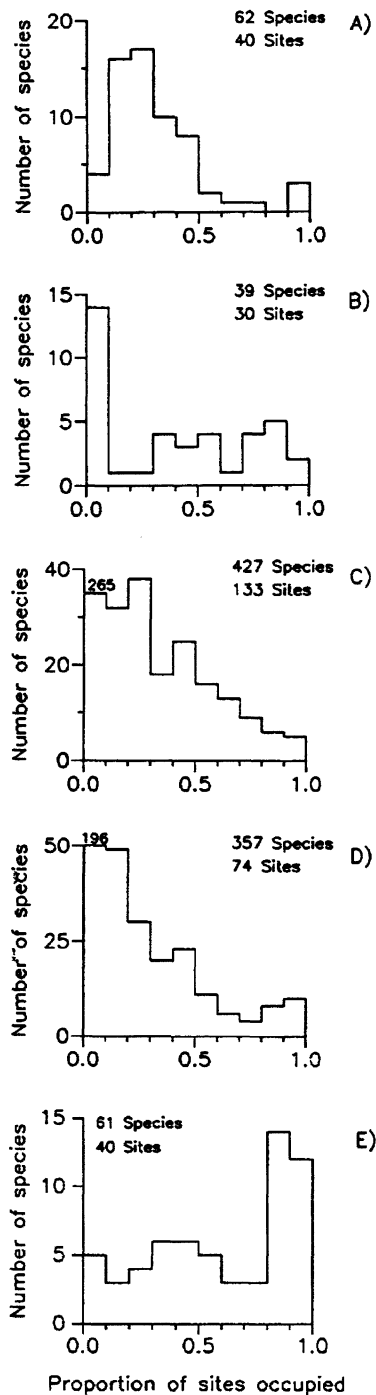
Fig. 4. Regional distribution of plant species in four vegetation types in North America. A. Tallgrass prairie (Minnesota to Oklahoma; Diamond & Smeins 1988). B. Trees in southeastern floodplain hardwood forests (South Carolina to Texas; Quarterman & Keever 1962). C. Trees and herbs in upland northern hardwood forests (Wisconsin, Iowa, and Illinois). D. Trees and herbs in boreal forests (Wisconsin, Minnesota, Michigan, and Ontario). E. Distribution of 61 species in 40 sites from a simulated coenocline based on the parameters in Gauch & Whittaker (1972).

of variability in species absolute abundances within a site over time (Wolda 1978), with stable sites having a lower average CV than unstable sites. At an intermediate scale, we can determine if the rank order of species abundances is persistent despite fluctuation in species absolute abundances over time. To determine if the order of dominance changes over time, temporal variability of rank abundances was measured by calculating a correlation matrix using Kendall's τ for all pairwise comparisons of abundance rankings for samples at a site over time. Variability was determined by the obverse $(1-\tau)$ of the average value of Kendall's τ for all pairwise comparisons so that low average values of τ represent low temporal variability. At the coarsest scale, only the presence/absence of species is persistent, and both rank and absolute abundances fluctuate over time. To measure persistence in species presence/absence, coefficient of community values (CC, Whittaker 1975) were calculated for all pairwise comparisons of samples at a site over time. The obverse of the average CC values provides a measure of temporal variation in presence/absence of species with low CC values representing low temporal variability.

Mean CV values ranged from 132 to 175% indicating a high degree of temporal variation of absolute abundance values over time (Table 1). The average abundance ranking using Kendall's τ was rather low (ranging from 0.33 to 0.43), suggesting that the rank order of abundances was also variable. The obverse of the CC values ranged from 0.16 to 0.22 (Table 1). Values in this range have been interpreted to indicate high floristic stability in randomly located samples (Gauch 1982), but the data used here were recorded in permanently located quadrats which should increase floristic stability. These CC values reflect a mean turnover of 8-9 species /50 m^2 /yr (Glenn & Collins 1992). In conjunction with studies on spatial variability at Konza Prairie (Collins & Glenn 1991), these results demonstrate that the composition and structure of prairie vegetation is spatially and temporally dynamic.

Further aspects of the model to be tested would include the mechanisms affecting hierarchical structure. Two general mechanisms could apply. If the hierarchical structure is a function of different degrees of niche specialization, then the polymodal distribution pattern is best described by Kolasa's model. However, if the availability of habitats is non-random, then the model could reflect equal niche breadths among species, and the broad or local distribution of species would simply be a function of distribution of habitat types (Colwell & Futuyma 1971). This problem plagues all models of species distribution and abundance, not just the hierarchical continuum. Core species may produce this pattern by having broad ecophysiological tolerance and

Table 1. Variability in species composition and abundance over time at three analytical scales at Konza Prairie. Variation in absolute abundance is the mean coefficient of variation of cover values for all species at a site over time. Variation in abundance ranking is determined as the obverse of the mean Kendall's τ for all pairwise comparisons of species rank abundances at a site over time. Variation in presence/absence is determined by the obverse of the mean coefficient of community for all pairwise comparisons of presence/absence data at a site over time (see text).

Assemblage	No. of species	No. of years sampled	CV of absolute abundance	1-K.'s τ	1- Coeff. of community
1	100	8	152. 2	0. 41	0. 22
2	76	8	132. 8	0. 33	0. 16
3	98	9	150. 5	0. 38	0. 21
4	116	9	168. 6	0. 42	0. 20
5	123	9	174. 6	0. 39	0. 19
6	117	9	172. 3	0. 36	0. 22
7	131	8	157. 0	0. 43	0. 18

strong reaction (Clements 1916). This produces a positive feedback loop of site modification yielding conditions favorable to themselves from a broad range of initial conditions (Roberts 1987). Wilson & Agnew (1992) provide a detailed discussion of the concept of 'positive feedback switches' in plant communities. If dominant species do alter the environment in favor of their own persistence, then the notion of core species and switches (sensu Wilson & Agnew 1992) has important implications for community dynamics. Sampling a broad array of habitats for both vegetation and environmental variables, classifying these habitats and determining species distribution among habitat types would address the niche breadth versus habitat abundance hypotheses.

Discussion

The hierarchical continuum is compatible with much theoretical and empirical evidence from a variety of plant communities (e.g. Whittaker 1956; Werger, Louppen & Eppink 1983; Shipley & Keddy 1987; Itow 1991). The temporal variability of vegetation, an important component of the hierarchical continuum model, is often considered to be noise when classifying steady-state climax communities. Many vegetation classifications are based on single samples of species, primarily those of intermediate abundance and distribution. Widely distributed species are rarely used for classification because they provide no information for distinguishing among associations. Rare species contribute little to classifications because their presence could be little more than chance or noise (e.g. Westhoff & van der

Maarel 1973; Gauch 1982). These rare species, however, provide much of the structure, pattern, and diversity within the hierarchical continuum.

The dynamic nature of the hierarchical continuum implies that species will change their distribution and abundance patterns along the gradient in response to environmental fluctuations. At very small scales, there is clear evidence that plant communities are highly dynamic (van der Maarel & Sykes 1993; Herben et al. 1993). Measurement of patterns along short environmental gradients, e.g. lakeshores (Keddy 1983), floodplains (Menges & Waller 1983) will show high year-to-year variation in abundance and distribution of satellite species in response to numerous biotic and abiotic variables. Larger spatial gradients, e.g. latitudinal gradients, Diamond & Smeins (1988); mountain gradients, Peet (1981) will show slower fluctuations, primarily in response to a small number of abiotic variables such as growing season precipitation or mean annual temperature. Assuming distribution is positively correlated with niche breadth to some extent (Bock & Ricklefs 1983; Brown 1984), core and rural species will show relatively small temporal variability in response to environmental fluctuations by having broader niches which can incorporate these environmental fluctuations. Urban species with high population densities may exhibit large temporal variability as the environment fluctuates in and out of the specialized conditions to which they are adapted.

The hierarchical continuum concept incorporates Aarssen's (1983) theory of competitive combining ability in which species with similar niches increase their competitive ability over time. In support of Aarssen's model, Johansson & Keddy (1991) demonstrated that similar species are more equal in competitive ability than are dissimilar species. Tilman & Wedin (1991) provide further evidence by demonstrating that *Andropogon gerardii* and *Schizachyrium scoparium*, dominant grasses in the tallgrass prairie, are nearly equal competitors for soil nitrogen, the most limiting nutrient in prairies (Seastedt & Ramundo 1990).

Finally, the hierarchical continuum concept contributes a mechanistic and explanatory function to the notion of self-similarity in plant community structure as proposed by Collins & Glenn (1990). If widely distributed species are common in assemblages, then they should be common locally as well, and generally dominate at many spatial scales. Thus, the hierarchical continuum predicts a positive correlation between the rank abundance of a species at a small spatial scale and its rank abundance at a larger spatial scale (Collins & Glenn 1990).

Shipley & Keddy (1987) emphasized the need to test hypotheses derived from models of community struc-

ture. The hierarchical continuum is a concept that should be tested and refined. The concept is developed from a set of theoretical assumptions that are quite different from previous models of vegetation structure. Together, the community-unit, continuum, and hierarchical continuum concepts provide a framework for developing testable hypotheses in vegetation science. Such an approach may contribute to the resolution of the 'great debate' concerning the structure of plant communities along broad-scale environmental gradients.

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