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Community assembly rules, morphological dispersion, and the coexistence of plant species

Evan Weiher, G. D. Paul Clarke and Paul A. Keddy

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In order to find and define any assembly rules for communities, we must first investigate the patterns among species assemblages. We used a series of null models to test for patterns in wetland plant composition at the level of species, functional guilds, and traits. At the species level, we found significant checkerboard and nestedness patterns. Three functional guilds had some tendency to contribute a constant percentage to species richness, but after Bonferroni correction there was no significant pattern. Coexisting plant species showed no consistent overall pattern of morphological dispersion. However, when we considered each of 11 traits in turn, we found that 4 traits were overdispersed and 3 were underdispersed. Thus there are morphological assembly rules that constrain wetland plant community composition. These results reconcile contrasting views of community assembly. Communities can be simultaneously structured by a tension between two forces: abiotic external forces that constrain certain traits within limits and biotic internal forces that tend to keep coexisting species from being too similar. Because our sites vary along a fertility/disturbance gradient, we also investigated how trait dispersion varies in space. Trait dispersion increases with soil fertility; soil phosphorus explains about 36% of the variance in mean nearest neighbor distance. Species richness tends to decline with mean nearest neighbor distance, which contrasts with the general pattern for animal assemblages.

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A fundamental goal for the prediction and understanding of community structure is defining the rules that constrain how species are assembled into communities. Diamond (1975) first used the term “assembly rules” to address how different communities come into existence given a common pool of species. Since then, two paths of inquiry have predominated, both of which have relied on null, or neutral, models of community assembly.

The first path comprised the development of models that tested for patterns of species co-occurrence that differed from the null hypothesis that species are independent of each other (Connor and Simberloff 1979,

Simberloff and Connor 1981). Even though ecologists have been careful to note that many different causal factors can, in theory, lead to similar patterns of species associations (Connor and Simberloff 1979, Schlüter 1984), an unfortunate general perception is that null models seek to find evidence for competition. Null models actually test if patterns in community data show independence among species. While a lack of independence may imply that interactions such as competition may be important, the mechanisms causing the patterns must be shown using other methods. After several years of development, it was found that some null models incorporated so much biology into their assumptions

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that the likelihood of finding a significant result was very low (Colwell and Winkler 1984, Gilpin and Diamond 1984). However, the successful use of null models has shown that these problems can be overcome (e.g., Stone and Roberts 1990, Manly 1995). There is a growing consensus that many communities are structured by rules, and that at least some assemblages are more than random groups (Weiher and Keddy 1995, and references therein).

The second path of inquiry involves ecomorphological analyses, and considers the role of competition, the importance of limiting similarity, and the patterns consistent with them. There are numerous examples where these types of patterns have been found. For example, body size ratios are larger than expected by chance in desert rodents (Hopf and Brown 1986), and birds introduced to oceanic islands show morphological overdispersion (Moulton and Pimm 1987, Lockwood et al. 1993). There are also many examples where significant ecomorphological patterns were sought, but not found (e.g., James and Boecklin 1984, Rathke 1984, Scheibe 1987, and Simberloff and Boecklin 1991). Taken in whole, we must conclude that ecomorphological patterns exist, but are not ubiquitous (Weiher and Keddy 1995). One generality that has emerged is that there tends to be a positive relationship between species richness and the amount of morphological volume occupied in animal assemblages (Ricklefs and Miles 1994). For plant communities however, there are few demonstrations of ecomorphological patterns using null models. Rathke (1984) found that flowering phenologies among swamp plants tend to be more similar than expected by chance, while there are several cases where floral characters are overdispersed among congeners (Armbruster 1986, Armbruster et al. 1994).

Another type of ecomorphological approach that is based on limiting similarity involves the use of guilds. If limiting similarity controls community composition, then assemblages might be expected to have consistent proportions or numbers of species from different guilds. This approach has yielded some success (Fox 1989, Fox and Brown 1993), but the results have been contested (Wilson 1995, Stone et al. 1996). Constant proportions of species from guilds (guild proportionality) have been found in several types of vegetation (e.g., Wilson and Roxburgh 1994, Wilson and Whittaker 1995), but there is little evidence that this type of pattern is common.

The first path emphasizes patterns in species without consideration of ecological traits. The second considers traits, but only in the context of competitive exclusion. Here we begin with elements of both strategies, and extend them to explore general patterns of trait-dependent assembly of plant communities.

In this paper we have four major goals: (1) To test for patterns in plant communities at the level of spe-

cies, functional guilds, and traits, (2) to highlight the strengths and weaknesses of each approach, (3) to test each trait individually and allow for the possibility that different traits can either converge or diverge and therefore show independent patterns, and (4) to consider the role of environmental factors on patterns of trait dispersion.

The study site

We are working with wetlands primarily because of the well known variation in plant traits (Sculthorpe 1967, Hutchinson 1975, Shipley et al. 1989, Boutin and Keddy 1993) and the strong environmental gradients that are associated with community structure (e.g., Hutchinson 1975, Keddy and Reznicek 1986, Day et al. 1988, Moore et al. 1989). For this paper we focus on the herbaceous riverine wetlands along the Ottawa River, Canada. Community composition is related to (1) soil fertility/exposure to wave and ice scour and (2) elevation relative to water level (for a complete description see Day et al. 1988, Moore et al. 1989). The herbaceous wetlands considered in this study are found between the woody shrubs, at high elevations, and the emergent marsh (mixed emergent and submersed species). The wetlands within these limits vary from cattail marshes to wet sedge meadows to sandy beaches. All have minimal direct human disturbances.

Although the observations were taken in four wetland sites, significant variation occurred within each wetland site. For instance, while all wetlands have some species of cattail (e.g., *Typha angustifolia*, *Typha latifolia*, nomenclature follows Gleason and Cronquist 1963), three have large areas of cattail dominance. Similarly, three of the wetlands have sandy, infertile areas. The observations are species presences in 0.25-m² quadrats from the aforementioned papers (Day et al. 1988, Moore et al. 1989) plus 10 additional quadrats (from a low fertility area immediately upstream from a conspicuous promontory in one of the original sites). Standing crop and soil samples were taken, soil nutrients were measured at Agri-food laboratories using Standard Methods, and soil percent organic content was measured in our lab as loss on ignition at 550°C. Soil and community data are summarized in Table 1. We have used the term observation for quadrat throughout because we wished to use a general term that could apply to any sized observation unit, such as an island or a point.

The wetlands were sampled using a stratified random design. Sampling was designed to include the entire range of soil fertilities and elevations found along the Ottawa River. In each wetland complex, vegetation types were identified according to the

Table 1. Community and soil characteristics for 115 quadrats in Ottawa River wetlands.

	Mean	SD	Minimum	Maximum
Richness	7.94	3.65	3	19
Standing crop, g (0.25 m ⁻²)	137	96.6	0.72	432.9
Soil % organic content	12.2	11.01	0.36	54.3
pH	6.64	0.98	5.20	8.70
P mg g ⁻¹	9.68	5.89	1	34
N mg g ⁻¹	10.65	7.46	1.2	38.0
N/P ratio	1.14	0.70	0.182	4.80
Mg mg g ⁻¹	246.6	128.1	29	472
K mg g ⁻¹	89.3	53.1	10	267

amount of standing crop, and within these areas of relatively consistent standing crop, quadrats were placed at random coordinates. The objective was not to collect a random sample of wetlands in order to quantify the relative amounts of each vegetation type. Rather, samples were collected in order to minimize the peculiarities of the Ottawa River by including, more or less uniformly, all wetland types from infertile to fertile. Our bias, therefore, was toward uniform sampling. A completely random sampling approach would have biased the results toward the mean wetland on an aerial basis, and assemblages with high and low biomass might have been overlooked, or at least poorly represented. Under such an approach, our ability to draw general conclusions about wetlands would have been more strongly biased by the distribution of wetland types along the Ottawa River than in the more uniform sampling approach which we used. Even though we tried to control for bias, we should note that our results none the less are for Ottawa River wetlands and comparisons must be made with caution.

From this original data set, we found it necessary to exclude a set of observations because of several logistic constraints. In order to assess ecomorphological patterns, we needed to assign characteristic traits to species. Characteristic heights cannot be easily assigned to both aquatic macrophytes (e.g., *Elodea canadensis*, *Potamogeton robbinsii*), as their heights are dependent on water depth, and woody shrubs (e.g., *Myrica gale*, *Salix nigra*), because they have indeterminant growth. The removal of these observations limits our investigation to the herbaceous wet meadow. It also shortens the elevation gradient, which in some ways simplifies the analyses and interpretations. Another set of observations (24) were excluded because they had fewer than 3 species (this was necessary to allow the calculation of some of the test statistics, e.g., variance in nearest neighbor distance). These observations always included one large species (e.g., *Typha* spp., *Sparganium eurcarpum*, *Scirpus cyperinus*). It may be that in areas dominated by large species, the quadrat size was less than ideal. The exclusion of these quadrats also means that this study focuses on coexistence, rather than on patterns of dominance. In total, nearly 50% of the

original data set was excluded, leaving 115 observations.

This need for subsampling highlights the potential difficulties of using previously collected data. We might have ignored our existing data set, started from scratch, and set out quadrats in the wet meadow using the criteria outlined above. Does subsampling bias or invalidate our results? First, it is clear that our data are not a random sample of herbaceous wetlands. Second, any of the individual subsampling filters might seem acceptable, but taken as a whole, there may be a cumulative effect on the data set that is unknown and untestable. The main question is whether post hoc subsampling from an existing data set is fundamentally different from using a planned stratified random sampling design. It is clear to us that while some ecologists will find our methods acceptable, others will have severe reservations whether our data are valid or if our sampling methods caused untestable biases in the data. We can find no simple solution to this issue. Perhaps it is best to acknowledge it and let the reader decide. In the discussion we will point out that several of our general conclusions are not really affected by the possibility of sampling bias.

In order to further investigate the issue of sampling and bias, we repeated some of the analyses with two biased subsamples. To cause bias, we removed either the most fertile or least fertile 10% of the observations and reran some of the null model simulations. Please see the results section for more information.

The traits

We chose traits in order to capture as many functional and structural attributes of the species as possible, while pragmatically recognizing that we had to balance our list of desirable traits with the requirement that we measure them with replication in many species (Table 2). Thus, we omitted traits such as relative growth rate (Shipley and Peters 1990a, b), relative competitive ability (Gaudet and Keddy 1995), tissue nutrient content (McJannet et al. 1995), optimal temperature, root:shoot ratio, and palatability (Pacala and Tilman 1994), because of incomplete data or the difficulty of collecting

Table 2. The 11 traits measured on 88 species of wetland plants.

Trait	Description
Above ground biomass, g dry wt.	
Height of tallest photosynthetic tissue, cm	
Crown cover, cm^2	$((\text{diameter}_1 + \text{diameter}_2)/4)^2$ (Boutin and Keddy 1992)
Stem diameter, mm	
Capacity for lateral spread	$(\text{number of ramets}) \times (\text{distance to the furthest ramet, cm})$
Ability to spread with many close ramets ("tussockness")	$(\text{number of ramets or tillers within } 5 \text{ cm})$
Number of rhizomes or stolon apices	
Form index of leaf shape	$(\text{leaf blade area})/(\text{length from petiole to tip})^2$ (Goodall 1987) ¹
Leaf unit area, cm^2	per single leaf, measured with a planimeter ¹
Height plasticity	$(\text{variance of height})/(\text{mean height})$
Crown plasticity	$(\text{variance of crown cover})/(\text{mean crown cover})$

¹ a score of zero was given to species such as *Equisetum fluviatile*, *Scirpus acutus*, and *Eleocharis* spp. because they are photosynthetic cylinders (stems) and we chose not to measure the area of green stems.

such information. Consequently, our list of traits will appear to be less than exhaustive. Most plant ecologists would be able to suggest other traits that could be included. However, we think that it is important to move ahead and look for patterns using traits that we can reliably measure in a logically sensible amount of time.

Morphological plant traits are often strongly associated with functional characteristics (e.g., Horn 1971, Mooney 1972, Gaudet and Keddy 1988, Grime et al. 1988, Tilman 1988). This is often due to the trade-offs inherent in growth and development, as plants cannot allocate unlimited resources to every aspect of growth (Orians and Solbrig 1977, Bloom et al. 1985, Tilman 1988, Rees 1993). Other, less obvious trade-offs are also being found (e.g., colonization ability and competitive ability, Tilman 1987; genome size and frost resistance, MacGillivray and Grime 1995). There is growing evidence that the positive associations between plant form and function and trade-offs among traits mean that we may be able to use a few simply-measured morphological traits to capture a large proportion of species' functional attributes.

In order to assign characteristic traits to species, we collected data for 11 traits (Table 2) in 88 species between late August and early October, 1994 (in order to find specimens at their largest size, but before the onset of senescence). For each species we collected trait information on at least three individuals per wetland site. Because most species were found in only two of the four wetland sites, mean replication per species was 5.3 and the median was 6, which is similar to other studies of ecomorphological pattern. Individual plants were defined as ramets that were not obviously connected above ground. Individual plants were not chosen haphazardly, rather we used a semi-regular sampling method. In each wetland complex, we identified areas where each species was relatively common, and chose a large individual ramet near the center of its distribution along the elevation gradient. We also chose individuals at or near the

upper and lower elevational limits. This protocol was used in order to include a consistent measure of plasticity and minimize sampling bias. Occasionally, some species were not found in either sufficient numbers or over a broad enough elevation zone to allow for this sampling strategy. Two species (*Isoetes echinospora* and *Rumex verticillatus*) were not found in sufficient numbers, and an additional observation was added from a wetland complex immediately downstream from one of our sites. We initially wanted to log transform the data. This could not be done, because some traits have scores of zero. Adding one before taking the log is not reasonable here, as the transformation will alter the distribution in a way as to compress the lower values.

There is obviously some question regarding the validity of using characteristic traits for plant species. There are several points that should be raised. First, in herbaceous vegetation, plants produce iterations of ramets that are of determinate size (White 1984). Second, while plant size will vary from year to year, the among-species differences in size and allocation patterns are likely to overwhelm intraspecific variation. For instance, *Eriocaulon septangulare* is a seapose evergreen rosette that grows to only a few centimeters in height, while a sympatric species like *Juncus pelocarpus* is a rhizomatous equitant-leaved rush which tends to be about twice as tall. Similarly, most people can easily distinguish a cattail (*Typha* sp.) from an arrowhead (*Sagittaria* sp.). Other ecomorphological studies have often focused on fine-scaled trait differences within related taxa (e.g., passerine birds, Lockwood et al. 1993; granivorous rodents, Fox and Brown 1993), but we included the entire vascular flora. Third, we avoided traits that could not be repeatedly measured in a garden situation. In various pot experiments, we have found that many traits are highly correlated from year to year (e.g., height, biomass, leaf shape), but some are not (e.g., root:shoot ratio, percent flowering). Fourth, in studies

of ecomorphological dispersion in animal assemblages, museum specimens have often been used for collecting trait data (e.g., Miles and Ricklefs 1984, Shum 1984, Scheibe 1987, Lockwood et al. 1993). This means that the place and date of collection may have had little to do with the populations found in the study sites. For this study, an analogous approach would have been the use of herbarium specimens. Fifth, we recognize that phenotypic plasticity, to some extent, blurs our ability to assign characteristic traits to plant species. For this reason, we also included measures of plasticity (as the coefficient of variation) as separate traits.

The dimensionality of the trait data was reduced by using principal components analysis (PCA). We did this in order to compare the overall pattern of dispersion when the traits were made into composite uncorrelated principal components. The first four principal axes explained 87% of the variation in the 11 traits. The first principal component explained 48.8% of the variance and was strongly associated with overall size. The second principal component explained 16.4% of variance and was strongly associated with leaf shape and tussockness, as tillering is correlated with linear leaf form. The third principal component explained 13.6% of variance and was associated with traits that measure vegetative reproduction (number of rhizomes or stolons and the capacity for lateral spread, which is the product of number of rhizomes and the distance to the furthermost ramet). The fourth principal component explained 8.7% of variance and was associated with plasticity. Although stopping rules have recently been developed for PCA (Jackson 1993, Franklin et al. 1995, Mehlman et al. 1995), we included the first four components because each was strongly associated with different aspects of plant morphology. Although PCA can be used to untangle correlated traits, its use as a predictive tool is limited, as PCA-derived trait space will change with different species pools. We also wanted to investigate each trait in turn, which is of course not possible with PC scores.

Randomization models

We used statistics that were derived from three kinds of data: species data alone, functional guilds, and traits. The test statistics are described in more detail below. The main reasons for using different kinds of data as bases for test statistics were to compare the quantity and quality of information gained from each kind of test and to compare newer tests to older ones.

Randomization models were built following Noreen (1989). The observation matrix (observations by species) was randomized at least 5000 times. Row and column totals of the species by observation matrix were held constant (i.e., both the species richness of each

observation and the total number of times a species was observed were held constant).

Species statistics

Checkerboardness (C) was calculated following Stone and Roberts (1990). This statistic tests whether or not species co-occur less often than expected by chance. It is the updated version of many of the early tests for deviations from random expectation (cf. Gilpin and Diamond 1984) and it is analogous to an overall chi-squared test of species independence.

Standardized nestedness (N_s) was calculated following Wright and Reeves (1992). Nestedness is a measure of how well the low diversity observations can be considered as proper subsets of the higher diversity observations, that is, whether the relatively rare species tend to be confined to the highest diversity observations. Although developed for conservation purposes and usually applied to habitat islands, nested patterns can occur at various scales of observation (cf. Silvertown and Wilson 1994).

Guild statistics

Guild proportionality was calculated in a manner suggested by Wilson (1989). We have used the term "guild proportionality" to avoid creating new jargon and to facilitate comparisons, but we recognize that the strict definition of guild (sensu Root 1967, Simberloff and Dayan 1991) may not be easily applied to plants. Gitay and Noble (1997) have recently addressed the terminology surrounding the idea of grouping species according to their resource use, allocation patterns, and responses to perturbations. Our groupings are based on morphological traits (e.g., capacity for lateral spread and various size measurements) and operational traits (e.g., percent flowering in the first year), so that species with common character syndromes were grouped (Boutin and Keddy 1993). Because the species within each of our groups collect the same resources in the same way, the groups are best defined as functional guilds (Gitay and Noble 1997). The species within each group likely respond to perturbations in a similar manner, and also likely do so using similar mechanisms. If this is true, then according to Gitay and Noble, the groups might also be called functional groups.

We followed the decision rules for assigning species to functional guilds as described by Boutin and Keddy (1993) for riverine wetland plants. Guild proportionality determines whether the proportion of species from each guild tends to be more constant than expected by chance (Wilson 1989). This was done by comparing the among-observation variance in the proportion of spe-

cies from a guild to the variance after the observation matrix had been randomized. Variances smaller than expected by chance denote significant guild proportionality.

Trait statistics

To investigate the morphological dispersion of species in trait space we followed the reasoning of Ricklefs and Travis (1980), Travis and Ricklefs (1983), and Moulton and Pimm (1987). Testing for patterns in morphological dispersion is analogous to the question of spacing patterns of individual plants (i.e., regular, random, or clumped distributions). When assessing patterns in physical space, the locations of individuals can be shown in map form and patterns can be assessed. Similarly, evaluating ecomorphological patterns relies on the locations of species in trait space. A simple example would be to plot species in two dimensions (Fig. 1, the traits could be height and leaf shape). Trait dispersion has three basic components that can be measured. The first component is the area or volume of morphological space occupied by the species in the observation. In Fig. 1 the species in observations 1 and 2 clearly take up more of the available space than do the species in observation 3. The second component is how densely packed the species are, or how close their nearest neighbors are. The nearest neighbors in observation 1 have much larger mean distances between them than do the species in observation 2 or 3. The third component is the evenness of species packing. Again, observation 1 has much more even species packing than do the other observations. Finally, observation 1 shows classic limiting similarity, with a large volume of trait space occupied, with low and even density of species packing.

We used the mean nearest-neighbor Euclidean distance (meanNND) in order to assess the density of species packing (following Ricklefs and Travis 1980). We also noted the minimum nearest-neighbor distance (minNND) to test for absolute limits to similarity among coexisting species. For evenness in species pack-

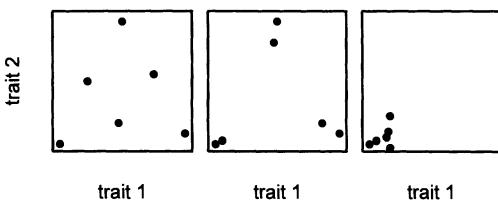


Fig. 1. Three possible assemblages of six species, plotted in two-dimensional trait space. Each shows a different pattern of trait dispersion. Assemblage 1 occupies a large area (or volume), and has large, even nearest-neighbor distances which are indicative of limiting similarity or overdispersion. Assemblage 3 occupies a small area, with small uneven nearest neighbor distances which are indicative of clumping or underdispersion. Assemblage 2 is intermediate.

ing, we have simply used the variance in the nearest neighbor distances (s_{NND}^2), where a significantly small variance means even species packing. Rather than resorting to a complex algorithm to compute an n-dimensional volume, we simply used the mean Euclidean distance among species (meanED) as a general indicator of the volume of trait space occupied. Although this is most likely an imperfect measure, small mean distances between species indicate that the species are clumped in one section of the trait space and that they do not take up a large fraction of the available volume.

We have divided the trait-based tests into two categories: n-dimensional tests of overall pattern, explained above, and one-dimensional tests of trait-specific pattern. For the n-dimensional tests we used the first 4 principal components of the 11 traits. Because significant patterns in different traits could potentially cancel each other and lead to the acceptance of the null hypothesis when there are indeed patterns, we also included one-dimensional, single trait tests. To assess species dispersion for each trait, we used the same measures for the density and evenness of species packing as those described above. For the volume of trait space occupied, we used the range of values (maximum value minus the minimum value), because it is simpler and more accurate than using the mean Euclidean distance. The trait statistics were also tested for constancy, as in the guild proportionality tests. If the among-observation variance was smaller than expected by chance, then that statistic can be considered a constant assembly rule. Finally, the maximum and minimum values of each trait were determined for each quadrat and these were also tested for constancy.

Alternative hypotheses and probabilities

Checkerboard, nestedness, and guild proportionality tests were calculated as one-tailed tests. Tests for nearest neighbor distance and morphological volume were calculated as two-tailed tests because we were interested in results that were either greater or less than what might be expected from chance. Exact probabilities for the hypothesis that the test statistic was as large as it was found to be, given random expectation, were calculated as:

$$p = \frac{((\text{the number of times the randomized statistic} \geq \text{actual statistic}) + 1)}{(\text{the number of randomizations} + 1)}$$

(Noreen 1988). The greater than sign was simply changed to a less than sign for calculating the probability of an alternative hypothesis, that the test statistic was as small as it was found to be, given random expectation. These probabilities were determined using separate randomizations.

Table 3. Checkerboard and nestedness scores and probabilities for 88 species of wetland plants in 115 quadrats. The species by observation matrix was randomized 10 000 times for each test.

	Value	Probability
Checkerboardness, C	65.76	0.0001
Nestedness, N _s	0.1686	0.0001

Each probability determined by a randomization procedure is best thought of as a significance level – “a summary statistic giving a weight of evidence against the null hypothesis” (Kempthorne and Doerfler 1969). In the tables and figures, we have marked the results that we consider highly significant in bold. Because in some instances we performed the same test for either a series of functional guilds or a series of traits, we also included sequential Bonferroni corrections (Sokal and Rohlf 1995).

We used Manly's RT program for testing the significance levels of linear relationships (Manly 1994). The program uses Monte Carlo methods to compute exact probabilities for least squares regressions. SigmaStat was used to compute r^2 .

Results

Patterns in species occurrences

We found significant non-random patterns in terms of checkerboard score and standardized nestedness (Table 3). Significant checkerboardness means that some species are found together less often than would be expected by chance alone. One way of interpreting this result is that wetland plant communities are assembled by rules that tend to limit the co-occurrence of some species. Significant nestedness means that the probability that the least common species will be found in observations with relatively high species richness is about 0.16, which is greater than what would be expected by chance. Similarly, in observations with low species richness, there is a disproportionately high occurrence of common species. Neither of these results provide any explicitly defined assembly rules.

Patterns in functional guilds

Three functional guilds: matrix dominant (which are large species capable of high rates of vegetative spread), interstitial clonal (which are small species with moderate crown cover and vegetative spread), and facultative annual (which are perennials capable of high rates of flowering in the first year of growth) had a tendency to make up a relatively constant proportion of the species in each observation (Table 4). However, Bonferroni

corrections make the significance levels insufficient to reject the null hypothesis at $\alpha = 0.05$. The α would need to be raised to over 0.1016 to reject the null hypothesis.

These results point to the strengths and weaknesses of this approach. First, testing multiple hypotheses requires very high significance levels to overcome Bonferroni corrections. Because species are assigned to functional guilds in a somewhat subjective manner, small errors in assignment could have a great effect on the results (see also Fox and Brown 1993). On the other hand, the potential utility of such rules is great. If we had rejected the null (by increasing α), then we would have an explicit assembly rule: 19.6% of species in a quadrat should come from the facultative annual functional guild. This has the clear appeal of potentially providing a simple rule.

General patterns in traits

The n-dimensional tests showed that coexisting plant species have a slight, but non-significant, tendency to be overdispersed in trait space (Table 5). There may be a limit to the minimum morphological distance between coexisting species. Thus, there is more evidence to suggest that coexisting plant species are limited by similarity than the converse, that environmental factors act like sieves or filters (sensu Southwood 1977, Keddy 1992).

Specific patterns for different traits

Of the 11 traits, 4 were overdispersed while 3 were underdispersed (Table 6). Bonferroni corrections had little effect on the results because the significance of the patterns was very strong. This mixture of patterns likely caused the lack of significant overall pattern found in Table 5. Note that all the overdispersed traits relate to size, and therefore had heavy loading on only the first principal component. The underdispersed, or clumped, traits included one trait related to size (crown cover) and two that were largely unrelated to size: height plasticity and tussock score.

For the overdispersed traits, significant patterns were most evident for the mean nearest neighbor distances. The volume of morphological space had weaker patterns, as judged by the significance levels. There was no tendency for traits to have even species packing (not shown). For the underdispersed traits, patterns were most significant for the volume of morphological space, as opposed to nearest neighbor distances.

Several of the trait statistics had an among-observation variance that was significantly less than expected by chance (H_3 , Table 6). Because of their low variance, the values of these statistics are tightly constrained. More importantly, they might also be considered as assembly rules. Several trait maxima and minima also

Table 4. Mean guild proportions, guild proportionality scores (variance in guild proportion), and probabilities for 88 species of wetland plants in 115 quadrats. H_1 tests if the among observation variance is smaller than what would be expected by chance. The species by observation matrix was randomized 10 000 times for each test.

Functional guild (guild)	Proportion of species in F.G.	Mean guild proportion	Variance in guild proportion	H_1 : constant proportion
F.G.s from Boutin and Keddy (1993):				
matrix dominant	0.090	0.180	0.0135	0.0334 ¹
matrix tolerator	0.068	0.082	0.0131	0.9683
interstitial tussock	0.136	0.153	0.0199	0.9500
interstitial clonal	0.181	0.134	0.0135	0.0401 ¹
interstitial reed	0.125	0.138	0.0194	0.8962
facultative annual	0.159	0.196	0.0138	0.0127 ¹
obligate annual	0.147	0.061	0.0103	0.9106
isoetid	0.068	0.051	0.0077	0.7881

¹ with a Bonferroni correction (approximated by $\alpha/8$ functional guilds = 0.006) these would be viewed as non-significant.

had among-observation variances that were less than would be expected by chance. These putative assembly rules are shown in Table 7. Although the mean nearest neighbor distances for both the number of rhizomes and the tussock score tended to be constant, they were not included in Table 7. Both of these traits are simply counts, and therefore any consistency in nearest neighbor distance might be considered as trivial and expected.

Patterns along gradients

Our observations were made over a reasonably wide fertility/exposure gradient (see again Table 1), and it is possible that the distribution of quadrats along the gradient affected our outcome. Our sampling was not absolutely uniform across the gradient, therefore we may have more quadrats from one qualitative wetland type than from others. This means that our results may be biased toward describing an observation with characteristics that are similar to the mean characteristics of our sites. Therefore the overall results may be inappropriate for describing the patterns at the ends of the gradient.

In order to address this, we subsampled our data by first omitting the quadrats with highest soil fertility to create a low fertility biased data set, and then creating a high fertility biased data set. We then reran the simulations for single trait nearest neighbor tests. In general, the results were unchanged, although there were occasional losses of power (i.e., p increased slightly). This suggests that our results are somewhat robust to any sampling bias along the fertility gradient.

We also investigated for possible effects of position on the gradient(s) on trait dispersion to see if dispersion varies in a predictable manner. Prediction of trait

dispersion is a potentially powerful tool for defining assembly rules. Although pattern detection is a reasonable first goal for assembly rules, we also need to define the rules once we have detected their existence.

We used simple linear regression to seek predictive relationships between the environmental variables listed in Table 1 and trait dispersion in PCA collapsed trait space. We were not seeking to build an entire assembly model, but rather, we were attempting to determine if part of an assembly model might incorporate the prediction of trait dispersion from environmental factors. Due to multicollinearity in the soil data, we were faced with again using PCA to extract uncorrelated environment axes (Philippi 1994). Rather than further abstracting the results, we instead opted to simply choose the best single predictor of dispersion by graphically comparing the relationships.

Soil phosphorus was the best single predictor of nearest-neighbor distances in PCA trait space ($r^2 = 0.364$, $p = 0.0001$, Fig. 2). There was a weaker relationship between soil P and the volume of morphological space (Fig. 2, $p = 0.0001$). To our knowledge this is the first case where trait dispersion has been shown to vary along an abiotic gradient. The result corresponds well with field experiments. Increased nearest-neighbor distances are expected to be the result of competitive interactions and competition intensity increases with soil nutrients in these wetlands (Twolan-Strutt and Keddy 1996).

One might consider interpreting the increasing nearest-neighbor distances as being the result of increased competition for light (with available light at the soil surface decreasing with soil fertility). Indeed, Twolan-Strutt and Keddy (1996) did find that it was largely above-ground competition that increased along the soil resource gradient. Furthermore, the traits we used were heavily biased toward the above-ground portion of the plants.

Table 5. Trait dispersion along the first 4 principal component axes of morphological space and probability values. H_1 tests if the statistic is smaller than would be expected by chance, while H_2 tests if it is larger. The species by observation matrix was randomized 5000 times for each test. Note that these are two-tailed tests; the statistics are the among quadrat means. MeanED is the mean Euclidean distance among neighbors, minNND is the minimum nearest-neighbor Euclidean distance, meanNND is the mean nearest-neighbor Euclidean distance, and s_{NND}^2 is the within quadrat variance in nearest-neighbor Euclidean distance.

	Statistic value	Probability		H_2 : large
		H_1 : small	H_2 : large	
Volume of trait space	meanED	0.386	0.7560	0.2282
Minimum species packing	minNND	0.125	0.9646	0.0328
Mean species packing	meanNND	0.2142	0.7638	0.2262
Evenness of species packing	s_{NND}^2	0.0197	0.2338	—

Discussion

Ecomorphological patterns and community assembly

Wetland plant assemblages are simultaneously overdispersed and underdispersed morphologically. This result means that morphological assembly rules are at work in these wetlands. The results suggest that community composition is constrained by two kinds of rules, both of which are instructive for understanding how communities are structured. Some assembly rules work like a sorting device, calling for an overdispersed mixture of trait values within a community. Other rules work like filters, allowing only those species with certain similar trait values into the community. These results recall the notion of capacity rules and allocation rules (Brown 1987), whereby environmental factors first limit community composition according to species capacity to inhabit a site, then interactions, through allocation rules, further limit composition. Nearly all of the focus in studies on assembly rules has been on overdispersion, limiting similarity, and the existence of allocation rules, but for plant communities, we must also consider the alternative kind of patterns and rules.

There have been few, if any, studies showing trait overdispersion in plant communities at taxonomic scales larger than congeners (Weiher and Keddy 1995). Pacala and Tilman (1994) used simulation models to show that limiting similarity should, in theory, exist in real plant assemblages. Our results show that this ecological pattern, which has been found in numerous animal assemblages (e.g., Hopf and Brown 1986, Moulton and Pimm 1987, Dayan and Simberloff 1994; see also references in Weiher and Keddy 1995), also holds true for plant assemblages. This is encouraging because plant and animal ecologists have tended to work with different paradigms (filters/templets/strategies versus chance plus limiting similarity). The paradigms are apparently not mutually exclusive. This also means that plant and animal assemblages may not be fundamentally different.

There may be a dynamic tension between the two main forces to which we have alluded. In Fig. 3, we show assemblages as balloons in two-dimensional trait

space. Trait dispersion varies in terms of volume (shown as the balloon area) and nearest-neighbor distance (balloon grid size shows the relative distances between species). For clarity, the grid patterns are even, but note that our results did not show even species packing. For wetland plants, overdispersion was predominantly due to increased nearest neighbor distances (shown as larger grid size in Fig. 3b). We found four size-related traits to have significantly large nearest neighbor distances, but only one of these also had significantly large “volume” (actually measured as the range, largest minus smallest). The most likely causes of overdispersion are competition or evolution of the species pool under competition (Colwell and Winkler 1984, Roughgarden 1989), but it is possible that other causes could lead to such patterns (Schluter 1984). Competition is a force that comes from within assemblages, keeping species morphologically distinct and decreasing the density of species packing. In other words, competitive interactions are like the pressure inside a balloon.

Underdispersion is predominantly due to decreased volume (shown as smaller balloon area in Fig. 3c). We found three traits to have significantly small ranges, and only one of these also had significantly small nearest neighbor distances. The most likely cause of decreased morphological volume is environmental filtering (e.g., Southwood 1977, 1988, Keddy 1992), where species lacking certain traits are excluded from an assemblage. Environmental filtering is an external force that compresses assemblages in morphological space. It is synonymous with the surrounding air pressure that limits balloon size by pushing against the internal pressure.

Our results mean that two views of community assembly (limiting similarity from competition and morphological convergence from environmental templates or filters) are not mutually exclusive and can operate simultaneously (Fig. 3d). Physical and/or evolutionary constraints mean that there are trade-offs between traits (and between abilities) such that trait combinations are limited (Grime et al. 1988, Tilman 1990, Rees 1993, Ricklefs 1996). Given the constraints on traits within species, and the tension between specialization and optimization, it would seem that we were bound to find both over- and underdispersed traits within communities.

Table 6. Trait dispersion and probability values for 11 untransformed traits considered singly. The species by observation matrix was randomized 5000 times for each test. H_1 tests if the statistic is smaller than would be expected by chance, H_2 tests if it is larger, and H_3 tests if its among observation variance is less than expected by chance. The statistics are the among-quadrat means. After Bonferroni correction, the two-tailed initial critical α becomes 0.00227 (0.025/11).

	Volume of trait space occupied			Species packing, nearest-neighbor distance				
	Value	Probability			Value	Probability		
		H_1 : small	H_2 : large	H_3 : constant		H_1 : small	H_2 : large	H_3 : constant
Overdispersed traits								
height	129.9	0.9996	0.0004	0.0002	18.6	1.000	0.0002	0.9984
shoot biomass	17.54	0.6284	0.3706	0.3218	2.74	0.9990	0.0006	0.9912
unit leaf area	93.77	0.9456	0.0524	0.0014	13.02	0.9992	0.0018	0.7508
stem diameter	33.94	0.9978	0.0028	0.0092	4.48	0.9980	0.0026 ¹	0.8476
Random traits								
leaf shape	63.62	0.1918	0.8176	0.9942	7.95	0.5734	0.4332	0.7488
capacity for lateral spread	101.9	0.9352	0.0628	0.0442	12.21	0.6066	0.3772	0.3082
number of rhizomes	3.66	0.2084	0.7828	0.7870	0.428	0.1280	0.8666	0.0002
crown plasticity	237.1	0.0986	0.8966	0.3824	31.60	0.7080	0.2948	0.4954
Underdispersed traits								
crown cover	398.9	0.0002	1.0000	0.4364	51.11	0.0694	0.9390	0.5120
height plasticity	13.65	0.0002	1.0000	0.2608	1.75	0.0496	0.9484	0.8722
tussock	4.87	0.0006	0.9994	0.9980	0.486	0.0002	1.0000	0.0002

¹ sequential Bonferroni correction provides $\alpha = 0.025/8$ (i.e., 8 tests remaining) = 0.0031.

Correlations with trait dispersion

Trait dispersion increases with soil fertility. This agrees with observations that the intensity of competition increases with soil fertility (Twolan-Strutt and Keddy 1996). It is not yet clear if the relationship between trait dispersion and competition intensity/resource levels is a general property of communities. There are few, if any, corroborating examples in the literature and it is premature to suggest a generality (see also Beck 1997). The investigation of community assembly remains focused on simple pattern detection rather than moving on to how patterns change along gradients.

An exception to this is the continued interest in how the density of species packing and morphological volume vary with species richness (as reviewed by Ricklefs and Miles 1994). They found that in animal assemblages, species tend to be added at the morphological periphery, so that morphological volume increases with

species richness. They cited no examples of plant communities. In our wetland plant community data, there is a weak negative relationship between mean nearest-neighbor distance and species richness (Fig. 4). This can be interpreted in two complementary ways.

The first interpretation is that as species are added to assemblages, they are added within set boundaries in morphological space, and thus the mean nearest-neighbor distances tend to decrease with diversity. The observations with highest richness do tend to have low nearest-neighbor distances (Fig. 4). Our results that show consistent trait ranges, maxima, and minima (Table 7) also support this view. The edges of assemblages may be relatively fixed in morphological space, and species are added, perhaps randomly, within these boundaries. The approximately lognormal distribution of morphological volumes with respect to richness does not contradict this view (Fig. 4). These patterns are dissimilar to those found in animal assemblages (compiled by Ricklefs and Miles 1994). If our results are confirmed in other vegetation types, then this difference may mean that animal and plant assemblages are subject to very different kinds of assembly rules.

The relationship between species richness and nearest-neighbor distance may also be interpreted as being due to the relationship between soil nutrients and nearest neighbor distance. Soil resources may set the level of above-ground competition intensity. Competition intensity may in turn control the level of limiting similarity, which can be measured as mean nearest-neighbor distance. Therefore, higher soil resources means greater above-ground competition intensity and

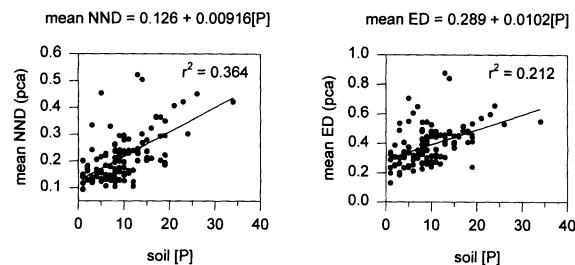


Fig. 2. Mean nearest-neighbor distance and morphological volume (as measured by the mean Euclidean distance between species) as functions of soil phosphorus ($\mu\text{g g}^{-1}$).

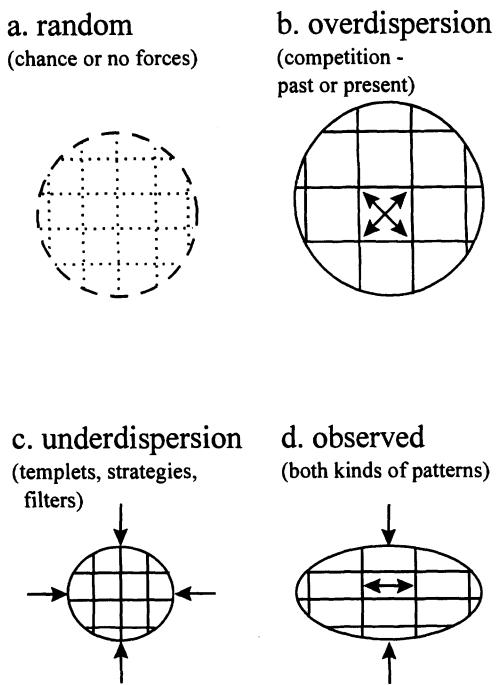


Fig. 3. A summary model showing the basic types of trait dispersion and the paradigms that are associated with them. Assemblages are shown as balloons in two dimensional trait space (axes are omitted). Morphological volume is shown as balloon size, and nearest neighbor distances are shown by grid size. Putative structuring forces are shown as arrows. Note that random, overdispersed, and underdispersed patterns were observed.

greater mean nearest-neighbor distance. Greater mean nearest-neighbor distance means that species richness will tend to decline, if morphological volume does not increase. With this view, the upper limit of species richness is a function of soil resources, mediated through mean nearest-neighbor distance.

These descriptions differ mainly in the priority of controlling factors. Pattern analysis, as presented here, cannot really distinguish between the two hypotheses.

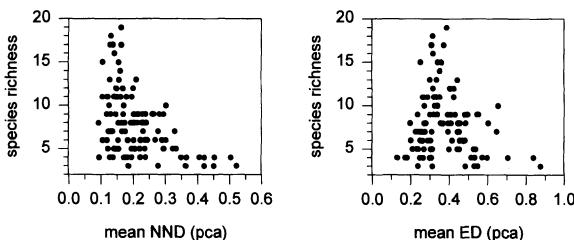


Fig. 4. Species richness as a function of mean nearest-neighbor distance and morphological volume. The choice of ordinate and abscissa is somewhat arbitrary, as either can be considered the independent variable.

Scale

The scale of the investigation may influence the kind of pattern that is detected. Among the Ottawa River sites, there is a distinct fertility/stress gradient, and coexisting species tend to show various amounts of trait dispersion. We do not yet know how dispersion might vary if we were to change the scale of our investigation. Observation size could be increased or decreased, or the number of wetland sites could be decreased or increased. Such changes might affect the conclusions that we draw. The scale at which we are currently working is larger than the within-community and within-patch approach taken by others (cf. Wilson and Roxburgh 1994), but it is smaller than macroecological and island biogeographical approaches often used by animal ecologists (cf. Brown 1995). Ecological patterns need to be studied at a number of spatial scales if we are to find clear generalities (O'Neill et al. 1986, Brown 1995).

The assembly rules

We used the reasoning behind Wilson's guild proportionality tests (Wilson 1989) to find patterns of constancy in the presence of several traits (Table 7). Our purpose was to go beyond the identification of non-random patterns, and try to define some actual assembly rules. The rules listed in Table 7 are clearly not very compelling, and certainly should not be considered as sufficient. On the positive side, because the rules are based on traits, they are potentially generalizable to other wetland species pools. However, the rules may be no more than simple descriptive expectations on the morphology of species that reflect the particular environmental constraints of the wetlands in our study. In other words, they may be a trivial and idiosyncratic consequence of our sampling scheme, and may not be transferable to other wetlands and species pools. Perhaps this is all we can expect from this type of assembly rule – constraints that have predictive power on a certain species pool within a particular range of environmental variables.

Another shortcoming of the putative rules is that they may have low predictive power. A statistically significant rule that has little predictive ability is of little use (like a regression with an r^2 of 0.05 and a p value of < 0.0001). The standard deviations around the leaf area rules in Table 7 are quite large proportions of the means. The rule regarding minimum leaf-shape may also fall under this category, but a more useful interpretation is that the rule simply calls for the presence of a species with either very long, narrow leaves or no leaves at all. When we seek assembly rules, we need to go beyond the recognition that patterns exist. We need to try to identify what the rules are.

Table 7. Putative assembly rules for riverine wetland plant communities. The rules apply to within quadrat (50×50 cm) patterns. Only those patterns that were viewed as significant after Bonferroni correction are given.

Putative assembly rules	Significance level
Range of heights (maximum – minimum) tends to be 130.0 cm (SD = 37.0)	0.0002
Range of leaf areas tends to be 93.8 cm ² (SD = 64.6)	0.0014
Maximum height tends to be 146.1 cm (SD = 39.7)	0.0002
Maximum leaf unit area tends to be 94.1 cm ² (SD = 64.7)	0.0030
Minimum leaf shape tends to be 0.1238 (SD = 0.27)	0.0008

Given the apparent difficulties associated with seeking constants in assemblages, we suggest that a better place to look for assembly rules is in how traits and dispersion vary along environmental gradients.

Conclusions

During the review process it became clear that some ecologists will have severe reservations whether our sampling and subsampling methods caused untestable biases, while others will find our methods reasonable. We can find no simple solution to this issue, except to openly report it to the reader. We also suggest that several points are robust to any sampling biases: (1) Ecomorphological methods tell us much more about assembly rules than do tests that are limited to species co-occurrence patterns. (2) Null models are powerful enough to overcome the problem of multiple hypothesis testing, given a large data set. (3) Assemblages can be structured by forces that simultaneously cause overdispersion in some traits and underdispersion in others (any sampling bias would tend to push our results one way or another, but not in divergent directions). (4) Trait dispersion, as measured by nearest neighbor distance, increases with soil fertility. (5) Unlike animal assemblages, we found no positive relationship between morphological volume and species richness and this could mean that assembly rules for plant assemblages are fundamentally different than those for animals. (6) The patterns caused by community assembly rules were abundantly evident, but the rules themselves remained elusive.

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