Journal of Vegetation Science 3: 147-156, 1992
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Competition and centrifugal organization of plant communities: theory and tests

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Abstract. The concept of centrifugal organization integrates community ecology's two main conceptual approaches: description of gradients and study of process. Centrifugal organization describes distributional patterns of species and vegetation types along standing crop gradients that are caused by different combinations of environmental constraints. Gradients radiate outwards from a single core habitat to many different peripheral habitats. The assumed mechanism is a competitive hierarchy where weaker competitors are restricted to the peripheral end of the gradient as a result of a trade-off between competitive ability and tolerance limits. The benign ends of the gradients comprise a core habitat which is dominated by the same species. At the peripheral end of each axis, species with specific adaptations to particular sources of adversity occur.

In wetlands, the core habitat has low disturbance and high fertility, and is dominated by large leafy species capable of forming dense canopies. Peripheral habitats are formed by different kinds and combinations of infertility and disturbance and support distinctive floras. The centrifugal organization model therefore allows us to predict the distribution of particular organisms (rare species) and to predict how changes to the conditions creating peripheral habitats will alter community composition.

Keywords: Competitive hierarchy; Gradient; Inclusive niche; Model: Rare species; Wetland.

Models of process and pattern

One of the challenges facing plant community ecology (and community ecology in general) is integrating two main conceptual approaches: description of gradients and study of process. For this, both pattern- and process-oriented models are required. Early work often emphasized description of patterns in community assemblages; now there is a growing need for process-oriented theory that can account for and predict such patterns.

Three well-known process-oriented models already exist (Austin 1986). One of these, proposed by Grime (1979), recognized changes in the species richness and species composition of herbaceous vegetation along gradients. The mechanisms underlying the pattern were stress and disturbance factors which reduced biomass and determined which ecological strategies were appropriate. This work is conceptually related to Southwood's habitat templets (Southwood 1977, 1988). Grubb (1977) emphasized the role of the regeneration niche in species coexistence. While the relative abundance of major plant species is probably controlled by interference competition for light, Grubb emphasized that patterns of coexistence, especially of minor species, are maintained by regeneration in different kinds of gaps. This work is closely related to studies of patch dynamics (Pickett & White 1985). The third model (Tilman 1982) proposes that the processes controlling plant community equilibria are based upon competition between species, each of which is limited by different resource ratios.

A fourth model, centrifugal organization (Keddy 1990) is based upon general empirical patterns in the distribution of species and vegetation types along gradients caused by different combinations of environmental constraints. The assumed mechanism is the development of competitive hierarchies with light as a limiting resource. We will begin by discussing the processes behind the model, then we will discuss the pattern of the model itself. We will also review some of the evidence we have for both the model and the mechanism. As well, there are several predictions made by the centrifugal organization model, and we will explore these by discussing conservation implications of the model.

Centrifugal organization

Starting with a single axis: Inclusive niches and competitive hierarchies

Inclusive niches are sets of niches in which all species perform best at the same end of the same resource gradient (Miller 1967; Colwell & Fuentes 1975). Plants, for example, all share a common requirement for a few basic resources; light, water and mineral nutrients. It therefore follows that most plants will grow their biggest, their fastest and will be most fecund where these basic resources are in greatest supply. Colwell & Fuentes (1975) provided many examples of inclusive niches.

Fig. 1A illustrates inclusive niches for species A to F, the far left end of the gradient being used by all. However, species A to F vary in their competitive ability with A on top being competitively superior and with F being subordinate. A trade-off is assumed here, between the ability to interfere competitively with neighbours, and the ability to tolerate adversity (sensu Southwood 1988) or stress (Grime 1979). The outcome of different competitive abilities and different tolerance limits is that species become differentially distributed along the gradient. This is illustrated in Fig. 1B where the horizontal dashed lines show the region from which a species is excluded by one or more dominant species. Fig. 1C shows a similar situation except that competitive exclusion is not complete. Near the limits of a species tolerance, the dominant is excluded by the adjacent subordinate. The distribution pattern remains the same however, except that in 1C, each species is displaced slightly up the resource gradient. This displacement of species appears to be resource partitioning, although here, the pattern arises from quite different mechanisms than are usually assumed (Keddy 1989). Mueller-Dombois & Ellenberg (1974) have similarly pointed out the importance of the distinction between physiological and ecological responses of plants when discussing causal origins of plant communities.

Multiple axes

When this basic pattern is extended to include many axes, there is then a pattern of centrifugal organization (Fig. 2). There are many peripheral habitats radiating outwards from the single, central core habitat.

A second assumption is now introduced: that the same species prosper at the benign end of the gradient, but that different species tolerate the adverse end. That is to say, the benign ends of many gradients are similar enough that we can describe them as a 'core' habitat which can be dominated by the same species. But at the peripheral end of each axis, species with specific adaptations to particular sources of adversity occur.

Example I

The term centrifugal organization was first used by Rosenzweig & Abramsky (1986) while studying the spatial distributions of two gerbil species in an Israeli desert. They set up homogeneous grid systems at a number of sites on stable and unstable dunes. These grids were censused using live traps every three months for 9 to 15 months. Rosenzweig & Abramsky (1986) observed that the first species, *Gerbillus allenbyi*, is most abundant in the productive regions in strips bordering oceans. Its populations are initially small in sparsely vegetated sites, then increase with increasing vegetation. The second species, *G. pyramidum* is abundant in sparsely vegetated sites; it reaches peak density

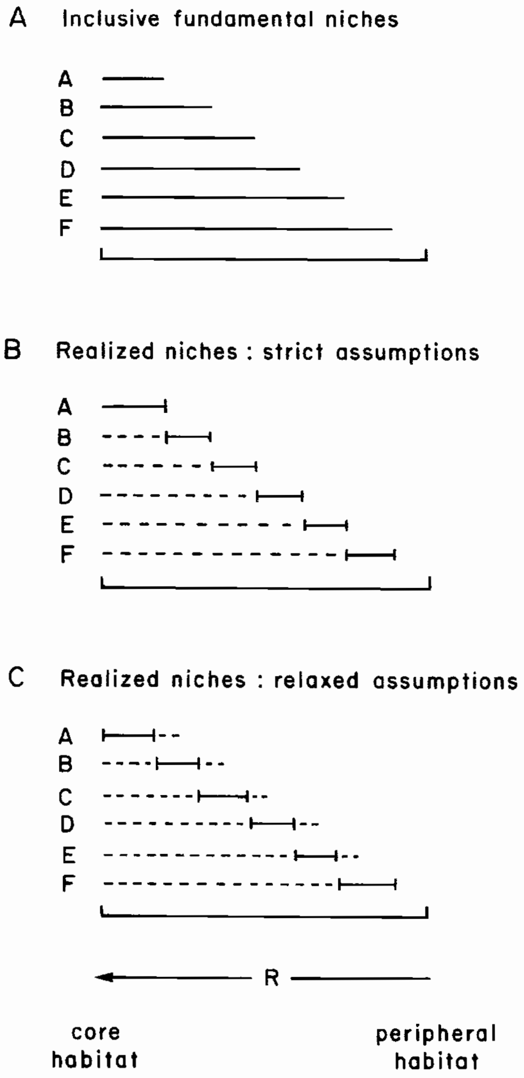

Fig. 1. Competitive hierarchies along a resource gradient. A. The gradient is shared by species A (dominant) to F (subordinant). B. Species are differentially distributed along the gradient with dominant species excluding subordinants — indicated by a horizontal dashed line. C. Competitive exclusion is incomplete with subordinant species excluding dominants near their tolerance limits. (After Keddy 1989.)

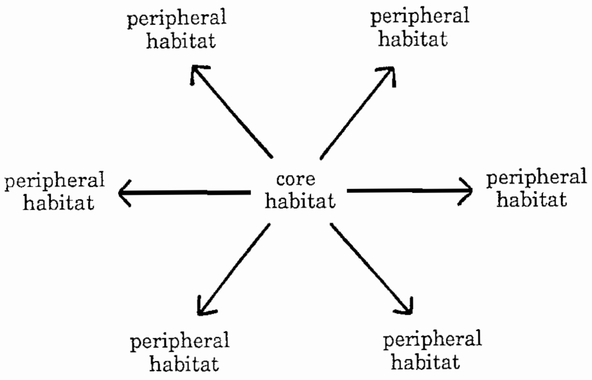

Fig. 2. Many resource gradients and the pattern of centrifugal organization.

at moderate vegetation density, and decreases in density as vegetation cover increases. Both species occur in high numbers in the regions of intermediate vegetation cover. This inclusive niche, or core habitat, is a region of both high seed production and protective plant cover, two important resources for seed-eating gerbils.

The key feature of this distribution is that there is a preference by both species for the core habitat but that their secondary preferences are distinct. This is the essence of centrifugal organization (Fig. 3). At low population densities, both species use the central habitat type. As their densities grow, they move out in different directions toward peripheral habitats within which they are the best competitor. To the right, *G. allenbyi* dominates where plant densities are higher, withstanding smaller abundances of seeds. To the left, *G. pyramidum* encounters more seed and can deal with a lack of shelter. Removal experiments could verify the role of competition in forming this pattern.

Example II

Feinsinger (1976) described a nectarivorous bird community in Costa Rica where the species have inclusive niches along a composite gradient incorporating aspects of nectar availability. This community is structured by the presence of one species, *Amazilia saucerottei*. This large hummingbird dominates regions with rich food sources and alters the foraging patterns of all other nectarivorous species. There was a clear hierarchy where *A. saucerottei* excluded *Chlorostilbon canivetti* which in turn excluded *Colibri thalassinus*. Other peripheral nectarivorous birds in the community structure themselves around these core species (Feinsinger 1976).

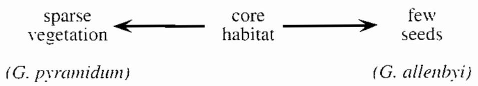

Fig. 3. The distribution of two species of *Gerbillus* and the pattern of centrifugal organization.

Further examples of such apparent hierarchies are cited in Morse (1974). However, interpreting such examples is often difficult since it is not always established whether there is a true core habitat - that is, a region preferred by both species. Similarly, removal experiments, which would test for inclusive niches and verify the role of competition in structuring the community, are often not performed (Keddy 1989). Thus, both the existence of core habitats and competitive hierarchies often rests on inference rather than on sound experimentation. Nevertheless, examples which appear consistent with centrifugal organization can be found in the literature (e.g. Culver 1970; Fellows & Heed 1972; Johnson & Hubbell 1975; Wolf, Stiles & Hainsworth 1976).

Example III

Keddy (1990) and Keddy & MacLellan (1990) have extended the centrifugal organization model to more complex communities by including more species and more peripheral habitats. Entire environmental gradients, or niche axes, radiate outwards from the central preferred habitats. Near the centre, species may have entirely inclusive niches, but nearer the periphery, niche overlap decreases until the end of the niche axis where only one species remains.

In wetlands, the central habitat has low disturbance and high fertility, and is dominated by large leafy species capable of forming dense canopies (Fig. 4). In northeastern North America, *Typha* dominates the core niche by reducing light levels for subordinate species. Beyond the core, different constraints create radiating axes along which different groups of species and vegetation types are arrayed. Along an axis of fertility for example, that is highest in a fertile embayment and lowest at an infertile, open shoreline, the community composition changes from a high biomass *Typha* dominated wetland to a sparsely vegetated shoreline that is dominated by isoetid and insectivorous species (Moore et al. 1989), two groups of plants indicative of infertile conditions (Boston & Adams 1987; Givnish 1988).

Gradients of nutrient concentrations however, are only some of the many gradients that occur in wetlands. Others are gradients of disturbance and the species found along these gradients differ from those found along gradients of fertility. *Typha* would again occupy fertile, protected areas, but where ice scour or severe

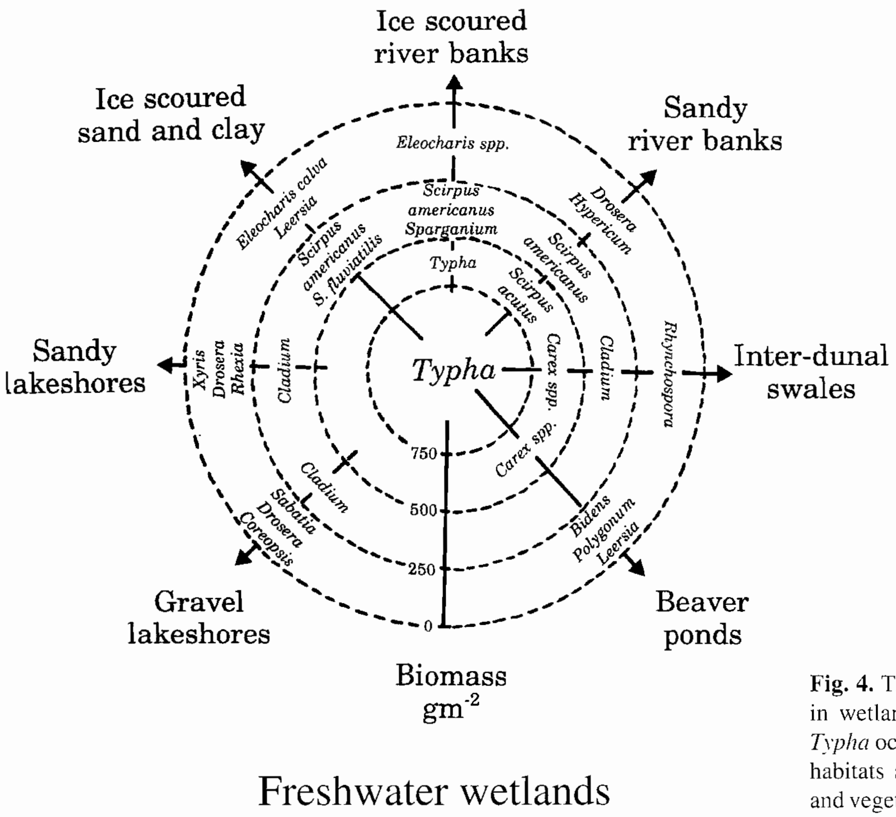

Fig. 4. The pattern of centrifugal organization in wetlands. Large, leafy dominants such as *Typha* occupy the core habitat while peripheral habitats are occupied by a variety of species and vegetation types. (After Moore et al. 1989.)

flooding occurs, either reeds or annual species would be abundant (Day et al. 1988; Moore et al. 1989). The deeply buried rhizomes of reeds protect them from moderate ice scour while fast growing annuals are able to set seed between periods of mud deposition (Grubb 1985; Day et al. 1988). Peripheral habitats that are formed by different kinds and combinations of infertility and disturbance support distinctive floras that reflect differing environmental conditions, e.g. shoreline fens (Charlton & Hilts 1988), interdunal swales and sand spits (Reznicek & Catling 1989), coastal plain wetlands (Keddy & Wisheu 1989), and river banks (Brunton & Di Labio 1989; Nilsson et al. 1989).

Evidence for inclusive niches and competitive hierarchies

The centrifugal organization model suggests that in the wetland communities that have just been described, species occur along inclusive niches, that there are competitive hierarchies, and that competition is most intense in the high biomass core habitat.

Unfortunately, many experiments do not test these ideas since plant species are usually grown only in relatively benign environments. The experiments do not extend past the region where the dominant species occur so they do not reflect the full range of conditions that exist along natural environmental gradients. Nor do they detect competitive refugia, regions where subordinate species survive in the absence of dominants (the right side of Fig. 1). Contrary to Tilman & Wedin (1991) who suggest that "There is little reason to discuss interspecific competition in a habitat in which a species cannot survive in monoculture", we believe that precisely such conditions must be included for inclusive niches and competitive hierarchies to be found.

Fig. 5 illustrates this point further. Let us consider how competitive relationships between two species might change along an environmental gradient. Since most experiments are still substitutive 'diallel' designs rather than additive designs (sensu Harper 1977), we will imagine the results of a substitutive design (although in practice, the results of an additive design would be similar and simpler to interpret). Relative yield (= yield in mixture/yield in monoculture) is plotted in Fig. 5 for each species along an environmental gradient for three different scenarios.

At the top is a diagram illustrating the results of a 'traditional' competition experiment where (1) the two species are, on average, similar in competitive ability and (2) no refugium exists. In the middle diagram we

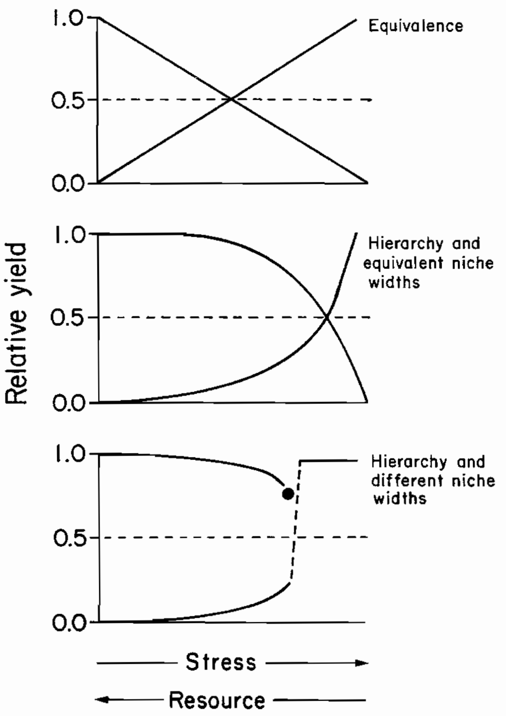

Fig. 5. Three patterns of competition experiments.Top: Species are similar in competitive ability and no refugia exist. Middle: Species are dissimilar in competitive ability and no refugia exist. Bottom: Species are dissimilar in competitive ability and have different tolerance limits. The near vertical dashed line represents a rapid transition in the relative yield of the competitively subordinant species as the dominant species approaches mortality.

allow for large differences in competitive ability and at the bottom we add major differences in tolerance limits. It is obvious that selecting the top situation precludes finding the bottom situation. As Keddy (1989) has argued, we can design competition experiments in such a way as to preclude discovery of competitive hierarchies along gradients.

Nevertheless, a number of experiments do provide evidence of inclusive niches and competitive hierarchies (Sharitz & McCormick 1973; Goldsmith 1973; Austin 1982) but only four such experiments that deal specifically with wetland habitats will be discussed here. The first examples test for the presence of inclusive niches and competitive hierarchies while the last two test for the presence of competitive interactions among pairs of species along environmental gradients.

Experiment I: testing for inclusive niches

To test for the presence of inclusive niches, Wilson & Keddy (1985) grew 12 different wetland species by themselves in 10 different substrates of increasing organic content. Although the species occurred at different points along the fertility gradient in the field, when moved into experimental conditions where there was no competition, 11 of the 12 grew larger in more fertile soil. Although actual field distributions differed, there was an inclusive niche at the organic end of the soil gradient.

Experiment II: a competitive hierarchy

Gaudet & Keddy (1988) investigated whether species inhabiting the inclusive part of the niche space are strong competitors by measuring and comparing the competitive abilities of 44 different wetland species in organic soil. Each of the 44 target species was grown in a pot with a phytometer, one species whose reduction in growth quantifies the competitive abilities of target plants (Clements & Goldsmith 1924). Both the target species and the phytometer were harvested at the end of the growing season. The target species that grew with the phytometer was a weak competitor when the phytometer's growth was similar to its growth when alone. Similarly, the target species was a strong competitor when the phytometer was suppressed.

The superior competitors were large wetland plants that shade subordinate species (Gaudet & Keddy 1988). Above-ground biomass and other simple plant traits such as height and canopy diameter accounted for 74% of the measured competitive ability. This general pattern is consistent with natural patterns found in wetlands; large, densely growing species occupy the fertile, undisturbed core habitats. *Typha latifolia*, *Phalaris arundinacea* and *Lythrum salicaria* are three species that grow in or near the core habitat and were among the top five competitors. Wilson & Keddy (1986) obtained similar results when, by measuring the position of plants in a competitive hierarchy, they were able to predict field distributions along an environmental gradient. Again, the better competitors occupied the fertile end of the axis.

Towards the core habitat there is a convergence towards a similar morphology; tall, fast growing competitive dominants, species which may be competitively equivalent (e.g. Ågren & Fagerström 1984; Aarssen 1989). Around the periphery however, there is a range of different habitats and a vast array of life forms and plant morphologies. Once the constraints of intense competition are released, a wide array of life forms becomes possible in response to the wide array of environmental conditions. For example, a variety of annuals occupy sites experiencing disturbance while a diverse group of isoetid and insectivorous species are typical of nutrient stressed sites (Grubb 1985; Boston & Adams

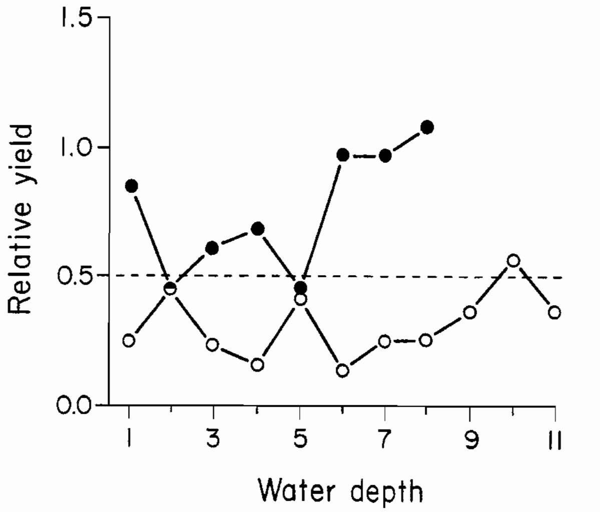

Fig. 6. The relative yield of *Typha latifolia* (closed circle) and *T. domingensis* (open circle) along a water depth gradient. (After Grace 1987.)

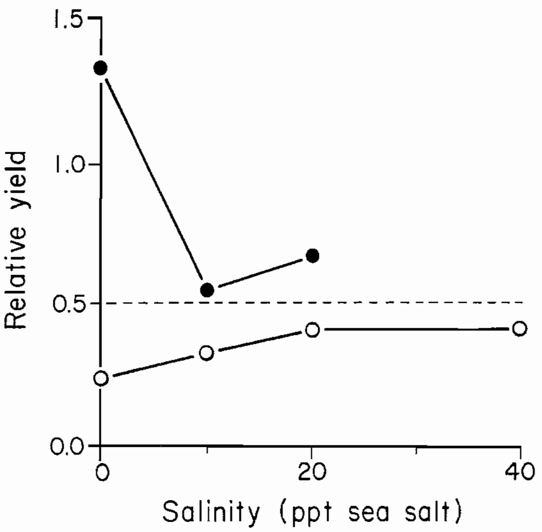

Fig. 7. The relative yield of *Typha orientalis* (closed circle) and *Juncus kraussii* (open circle) along a salinity gradient (After Zedler, Paling & McComb 1990.)

1987; Givnish 1988). Grime (1979) and Southwood (1988) have emphasized the general role of adversity and disturbance in life history evolution, and Grubb (1985) has emphasized the many finer-scale possibilities for specialization and niche differentiation within these two categories.

Experiment III: competitive interactions

Grace (1987) constructed an experimental pond and grew six-month old specimens of *Typha latifolia* and *T. domingensis* in monoculture and in mixture along a water depth gradient. Two years later, the relative yield of each of the two species was calculated by dividing the biomass of the species in mixture by its biomass in monoculture.

Relative yield values are only approximates of competitive ability but are here discussed since more direct measures are not available. When greater than 0.5, relative yield values indicated competitive superiority since the species grew better in the presence of a different species than it did in monoculture. Values less than 0.5 indicated that the species was competitively suppressed, while values of 0.5 indicated that a species grew equally well with either the same or a different species. *T. latifolia* seems competitively superior to *T. domingensis* in that its relative yield values were consistently at or above 0.5 (Fig. 6). *T. latifolia* was however, unable to survive in the deepest water treatments, so the deep water habitat was where *T. domingensis* could escape competitive domination.

Experiment IV: competitive interactions

A similar experiment using *Typha orientalis* and *Juncus kraussii* was performed by Zedler, Paling & McComb (1990) along a salinity gradient: either fresh, brackish, saline, or hypersaline. Four ramets of the two species were transplanted into either monoculture and mixed-species pots with different salinities. When grown in mixed-species pots in the fresh, brackish and saline treatments, *Typha* outgrew *Juncus* (Fig. 7). The relative yields of *Typha* were greater than 0.5, indicating that the mean total biomass of two *Typha* ramets in the mixed pots was more than half the biomass of four *Typha* ramets in monoculture. *Juncus*, with relative yields of less than 0.5, was suppressed. Adult plants of *Typha* however, were unable to survive in the hypersaline treatment, while specimens of *Juncus* could. The hypersaline treatment exceeded the tolerance limits of *Typha* and indicates a peripheral habitat where Juncus is no longer dominated by *Typha*, a situation depicted in the bottom of Fig. 5. Niche widths of the two species vary, so the subordinate species finds refuge in the peripheral stressed habitat.

Evidence for centrifugal patterns

Although preliminary work has shown that both wetlands (Keddy 1990) and forests (Keddy & MacLellan 1990) can be arranged into centrifugal patterns, objective tests are now needed to determine whether vegetation gradients do converge in core habitats. One approach would be to test whether, for a given range of habitats, the number of vegetation types varies inversely with biomass. If they are centrifugally arranged, vegetation types would be relatively similar to one another at high biomass, but very different at low biomass. Thus we can test for a predicted increase in vegetation similarity with increasing biomass.

Moore (1990) has done such a test, and has found such patterns. He used data collected from 15 different sites representing a wide array of biomass and vegetation types, including both lake-shore and riverine wetlands, high and low fertility wetlands, and different natural disturbance regimes. He began with three locations, a large marsh and sand dune complex on Lake Ontario and two locations on sand and clay along the Ottawa River, Canada (see further Moore & Keddy 1989; Moore 1990). In each location five sites were selected to represent five biomass levels, ranging from low (<150 g/m^2) to high (>1000g/m^2). Within each of these 15 sites 15 0.5 m × 0.5 m quadrats were randomly placed, species frequencies were measured in 9 subquadrats, and above-ground biomass harvested. Thus, the raw data matrix consisted of 225 quadrats, in which 141 species occurred with abundance values along a scale from 0 - 9.

The quadrats were ranked in order of standing crop, and mean dissimilarity of each quadrat to the 10 nearest neighbours (nearest in biomass, not spatial location) was calculated. Similarity was calculated with the quantitative, symmetrical index:

$$D_{jk} = 1 - 0.5\ [\min.\ (X_{ij},X_{ik})/(X_{ij})] + [\min.\ (X_{ij},X_{ik})/(X_{ik})]$$

This measure has a robust monotonic relationship with similarity even when species turnover between quadrats is high (Faith, Minchin & Belbin 1987). The Spearman Rank Correlation (Siegel 1956) was then used to test for a correlation between similarity and biomass. Moore (1990) found that the similarity of quadrats among sites was positively correlated with biomass (Fig. 8; p <0.0001). The null hypothesis can therefore be rejected.

As Moore pointed out, there are provisional aspects to this test. First, it is based on only 15 sites; one could argue that more high biomass or more low biomass sites might change the pattern; at the same time, these sites already present very different species composition and habitat types. Second, the patterns may be scale-dependent; Moore measured similarity based on 0.5 m × 0.5 m quadrats; different patterns may be found at larger scales. Third, the measure of similarity may be inappropriate. In fact, species similarities may not be the best measure of similarity. For example, two high biomass quadrats differing only in that they have different kinds of *Typha* (*T. latifolia* and *T. glauca* = *T. angustifolia* ×

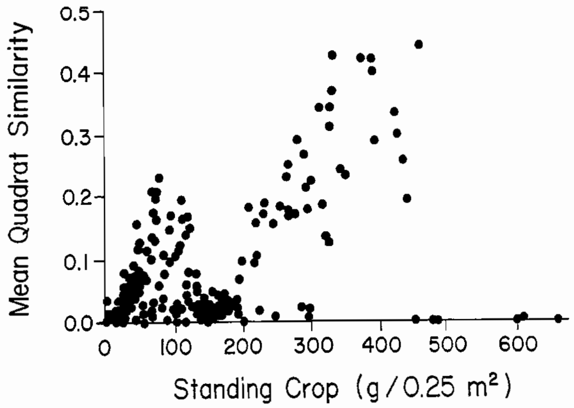

Fig. 8. Testing for centrifugal patterns in wetland vegetation. Mean interquadrat similarity plotted against biomass for 225 quadrats representing 15 sampling sites (see text). The increase in similarity of wetland vegetation types with increasing biomass is significant (Spearman's r_s = 0.39; p < 0.0001). (After Moore 1990.)

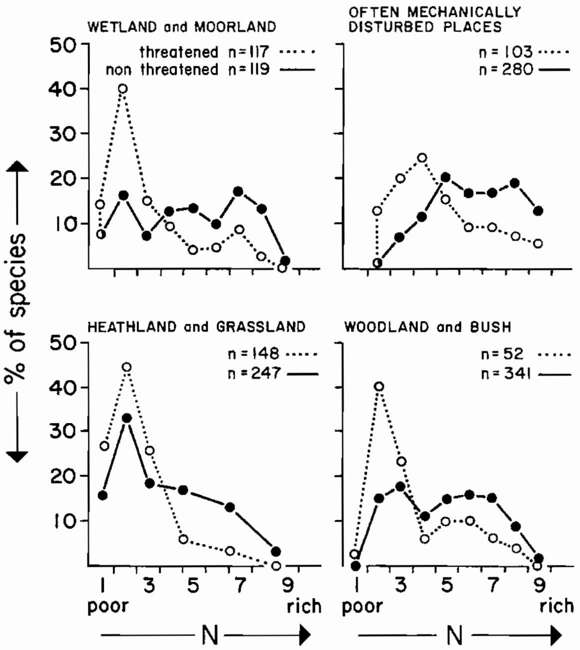

Fig. 9. Changes in density of threatened and non-threatened plant species along N, nitrogen gradients in four different European habitats. (After Ellenberg 1985.)

T. latifolia) would be classified as having little 'similarity', when in fact the species are similar in morphology and ecology. Yet they are treated as contributing to quadrat dissimilarity as a pair of species of widely contrasting ecology - say *Utricularia cornuta*, a carnivorous species, and *Nymphoides cordata*, a floating leaved aquatic. Thus, the best test might incorporate measures of similarity of form and function as well as taxonomic composition.

Predictions of the model

One feature of the centrifugal organization model is that it allows us to predict the distribution of particular kinds of organisms such as competitive dominants and rare species. An outstanding test of the prediction that rare species will be restricted to peripheral habitats is shown by Ellenberg (1988) which documents high numbers of rare plant species in the nitrogen-deficient regions of four very different habitats (Fig. 9). The restriction of rare plant species to low biomass, infertile wetlands has also been shown in North America (Moore et al. 1989). At the same time however, certain rarities might be excluded from peripheral regions. For example, rare species characteristic of mesic, remnant, old growth forests might be restricted to high biomass core areas (see Keddy & MacLellan 1990).

A second group of predictions of the centrifugal organization model deals with changes in sets of ecological communities in response to eutrophication. It is well known that eutrophication produces changes in individual plant communities, as documented in early work on the fertilization of dune communities (Willis 1963) and Tilman's (1982) re-analysis of the Park Grass experiments at Rothamstead. Wisheu et al. (in press) review the effects of eutrophication in wetlands, while current work is at a larger scale and compares infertile and fertile wetlands along the Great Lakes shorelines. The general trends which emerge with eutrophication are shifts in life form and species composition towards those forms and species associated with core habitats. That is, small plants are replaced by large canopy-forming species, and diverse communities are replaced by simpler ones. Over the landscape as a whole, through eutrophication peripheral habitats are removed and replaced by core habitats, which leads to an overall decrease in the diversity of wetland vegetation types.

The general sorts of predictions that can be made using the centrifugal organization model are summarized in Fig. 10. Both the number of vegetation types and the number of life forms and life history types should increase towards the peripheral end of resource gradients (Fig. 10A, B). Owing to the greater number of peripheral vegetation types, the species pool (the total number of species that inhabit a certain section of a resource gradient) also increases towards the periphery (Fig. 10C).

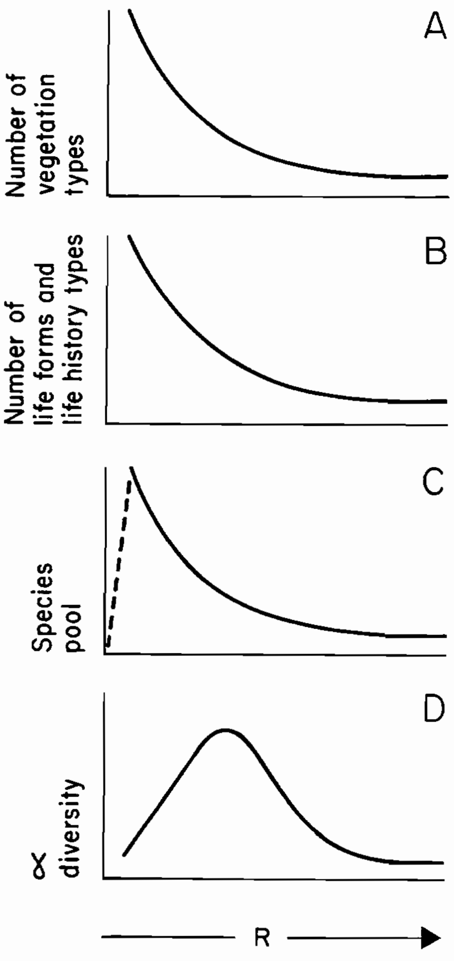

Fig. 10. Relationships along R, a resource gradient, predicted by the centrifugal organization model (After Keddy 1990.)

Fig. 10A-C contrast with Fig. 10D. Many examples (e.g. Al-Mufti et al. 1977; Willems 1980; Walker & Peet 1983; Vermeer & Berendse 1983; Wheeler & Giller 1982; Wilson & Keddy 1988; Moore & Keddy 1989; Wisheu & Keddy 1989; Shipley et al. 1991) support Grime's (1979) proposal that alpha (species) diversity is higher at 'intermediate' levels of biomass. Grime (1979) also describes changes in plant strategies which occur along this biomass gradient. The centrifugal organization model takes this well-known alpha diversity model for a single gradient and expands it to predict species richness and life forms at a much larger scale of organization: the landscape scale.

Conclusion

Centrifugal organization is one way of integrating the processes of competition and stress tolerance with the patterns of plant communities along environmental gradients. Future work could include testing the applicability of the model to patterns in other systems, or experimental testing for the proposed mechanism using other species and gradients. As well, one might ask whether other ecological or evolutionary processes differ between core and peripheral habitats. One might also wish to know why more competitive equivalents do not occupy some core habitats: certainly core habitats in forests appear to be more diverse than core habitats in wetlands. Further work is also needed to verify the predicted effects of environmental changes on community composition and the distribution of rare species and vegetation types in a landscape.

Acknowledgements. We thank S. Wilson for discussions, J. Hélie and P. Brunon for technical assistance and L. Aarssen, R. Bornkamm, J. Grace, L. Olsvig-Whittaker and a referee for reviewing the manuscript. We gratefully acknowledge funding from the Natural Sciences and Engineer Research Council of Canada and the World Wildlife Fund (Canada).

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Received 19 February 1991;
Revision received 16 February 1992;
Accepted 23 February 1992.