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Centrifugal organization in forests

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To date we have three process-oriented models of plant community composition: the plant strategy model of Grime, the regeneration niche/ gap dynamics model of Grubb and Pickett and White, and the resource ratio hypothesis of Tilman. A fourth complementary model, the centrifugal organization model is based upon general empirical patterns in the distribution of species and vegetation types along gradients caused by different combinations of environmental constraints. In this paper we explore whether this model, developed in temperate zone wetlands, can be generalized to terrestrial vegetation with woody species. We find that the mechanism of competitive hierarchies for light as a limiting resource is widely-accepted in forestry. Current descriptions of forest distributions along biomass gradients are also consistent with the patterns of the centrifugal organization model. We explore some apparent differences between forests and herbaceous wetlands, particularly the possibility that small scale gap dynamics are more important in productive forests than in productive wetlands.

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Introduction

Although plants make up 99.9% of the biomass on this planet, there are still no general predictive models for the assembly of plant communities, or models for predicting their responses to perturbation (Prentice and van der Maarel 1987). Recent approaches fall into two categories, depending upon whether they attempt to accurately portray pattern or process. Models of pattern predominate, and there is an extensive literature on quantitative techniques for describing vegetation, and on the limitations of these techniques (e.g. Whittaker 1967, 1975, Orloci 1978, Austin 1970, 1985, 1987, Minchin 1987). However, it is extremely difficult to make the transition from models of pattern to understanding of mechanisms, even when hypotheses about pattern are clearly stated (Shipley and Keddy 1987).

The ongoing debate about mechanisms underlying patterns of distribution on islands graphically illustrates the difficulties in inferring mechanism from pattern (Keddy 1989). An alternative is therefore to begin with hypotheses about mechanism as a basis for general models. To date we have three main process-oriented models of community composition (Austin 1986): the plant strategy model of Grime (1979), the gap dynamics/regeneration niche model (Grubb 1977, Pickett and White 1985), and the resource ratio hypothesis of Tilman (1982, 1985, 1988). A common theme among these models is that the competitive abilities of plant species interact with resource availability and disturbance to determine vegetation composition, with one of the key resources being light (Austin 1986). However, these more mechanistic models are not yet fully integrated with the more descriptive approaches which emphasize patterns. Such an integration may one day be possible, but at present these two approaches have been developing largely independently (but see Prentice and van der Maarel 1987).

The centrifugal organization model (Keddy 1989, 1990), aspects of which were first described for desert rodents (Rosenzweig and Abramsky 1986), describes patterns of vegetation along gradients and incorporates underlying mechanisms. In addition, it makes predictions about the distribution of both plant traits and

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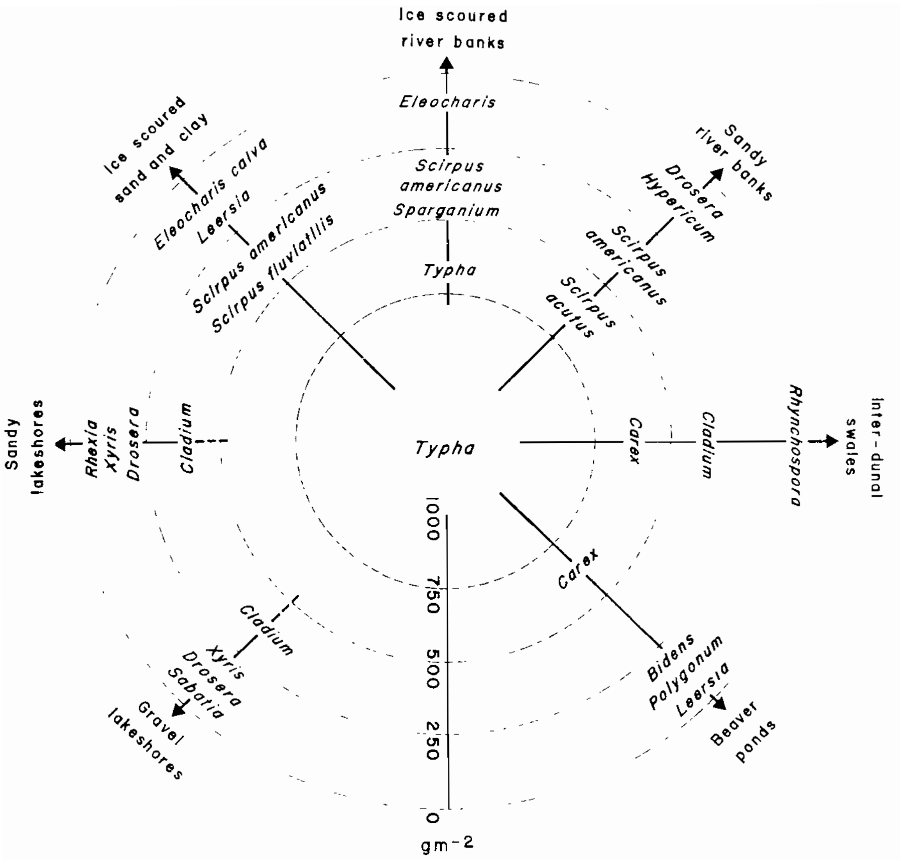

Fig. 1. Centrifugal organization of wetland plant communities. The high-biomass core region is dominated by a few canopy-forming, clonal perennials, primarily *Typha* species. Widely different plant communities radiate out along different constraint gradients (from Keddy 1989).

community attributes along environmental gradients. This model was formulated from patterns and processes observed in temperate zone wetlands. The objective of this paper is to explore the generality of this model, and its possible boundary conditions, by asking whether the patterns and processes summarized in the model can be extended to terrestrial vegetation and woody species. We will first briefly review the essential aspects of the centrifugal organization model, and then test whether the same patterns and processes can be found in temperate zone forests.

Pattern: centrifugal organization

The foundation of the centrifugal organization model is empirical (sensu Rigler 1982). It describes the distribution patterns of species and vegetation types along biomass gradients. Biomass gradients from wetlands across eastern North America tend to have similar vegetation at one end (the fertile, undisturbed end), but very different vegetation at the other end (the end with strong constraints of low fertility and/or high disturbance); this means that these varying gradients can be arranged as axes radiating out of a central habitat type of low site variation (Fig. 1).

These empirical relationships lead to qualitative predictions about higher order state variables (Keddy 1987, 1990). For example, the species pool, and number of life forms, is predicted to decrease with increasing biomass – that is, to increase towards the periphery of Fig. 1. Similarly, plant life forms vary predictably along biomass gradients, with large rhizomatous canopy-forming species restricted to core habitats.

Several of these patterns have now been confirmed. For example, rare wetland plant species are restricted to peripheral habitats where competition intensity is presumed to be lowest (Moore et al. 1989). In an extensive data set from Europe, Ellenberg (1988) has shown similar patterns in vegetation types ranging from wetland to forest, i.e. that rare species tend to occur in peripheral habitats. Moreover, his data verify an additional prediction: that the species pool should increase with decreasing fertility. However, we will not deal further with predictions and tests of them, since we are interested here in comparing and contrasting the patterns and mechanisms of centrifugal organization in marshes and forests.

Process: Competitive hierarchies and core habitats

Rosenzweig and Abramsky (1986) have postulated the existence of communities where there is shared preference for a productive central habitat, but where each species in the community is specialized upon a different secondary habitat (the secondary habitat being more "stressful" sensu Grime 1979, Rosenzweig 1987). This model can be extended by postulating that entire niche axes, or environmental gradients, radiate outward from this core habitat; this greatly increases the number of species which can be accommodated in such a model (Fig. 1). In wetland plant communities, the core of the model represents fertile, undisturbed habitats where a few large, rhizomatous species dominate (e.g. *Typha* spp.). As fertility decreases and disturbance increases to the periphery of the model, a much wider array of vegetation types exists, with different combinations of such constraints producing a diverse array of different low biomass vegetation types. Terborgh (1973) has also discussed this concept of core and peripheral habitats; he notes that islands of peripheral hibitat differ greatly among each other and have plant species with lower competitive abilities than core habitats.

An underlying mechanism of the centrifugal organization model is the strong interaction of plants for access to light. There is growing evidence that such interactions produce competitive hierarchies (Keddy and Shipley 1989, Keddy 1989); that is, that plants in natural communities can be ranked in order of competitive ability. Position in the competitive hierarchy has been shown to influence field distributions (Wilson and Keddy 1986a). Further it appears that the superior competitor is usually the larger plant. Evidence includes both a model (Givnish 1982) and a review (Keddy and Shipley 1989) of published pairwise competition experiments using vegetation types including sea cliffs (Goldsmith 1978), chalk grassland (Mitchley and Grubb 1986) and wetlands (Wilson and Keddy 1986a). Other evidence comes from the many transplant studies carried out by Clements and his co-workers (Clements et al. 1929, Clements 1933), from bioassays of competition intensity gradients (Wilson and Keddy 1986b) and from specific studies of the effects of height upon competitive ability (e.g. Givnish 1982, Gaudet and Keddy 1988, Keddy and Shipley 1989). There is also experimental evidence that above-ground competition is asymmetric whereas below-ground competition is symmetric (Weiner 1986). Such patterns follow logically from the observation that tall plants can shade short ones, but short plants cannot shade tall ones.

Given that all plants have shared requirements for a few essential resources (Grubb 1977, Harper 1977), we may logically expect that there will be inclusive fundamental niches along natural environmental gradients. In such circumstances, competitive hierarchies can determine species realized niches, and therefore distributions along environmental gradients (e.g. Miller 1967, Colwell and Fuentes 1975, Keddy 1989, Grace 1990).

While there is growing evidence consistent with this model (and its predictions), there is little evidence yet about the degree to which one can extrapolate beyond herbaceous wetlands. On one hand, the tendency for fertile, undisturbed sites to be dominated by a few genera of clonal plants may be a unique feature of wetlands. On the other hand, the underlying mechanisms of inclusive niche structure and competitive hierarchies for light probably occur in many other vegetation types. Added evidence for such generality can be found in Grime's (1979, 1987) proposal that fertile and undisturbed habitats should generally have lower alpha diversity than those with stress tolerant species. Similarly, Ellenberg (1988) has provided extensive empirical evidence that species pools are higher in low biomass habitats in a range of different vegetation types. We therefore examined the forestry literature to answer two questions: (1) is there evidence for competitive hierarchies in forests? (2) is there evidence for the patterns of centrifugal organization in species distributions along gradients? Three test cases have been chosen, the Alaskan taiga, the Great Lakes-St. Lawrence forest region, and the Great Smoky Mountains.

Evidence for competitive hierarchies in forest trees

Shade tolerance is the primary criterion used in forest ecosystems for arranging tree species into a competitive hierarchy (Horn 1971, 1981, Spurr and Barnes 1980), with the most shade tolerant species at the top of the hierarchy. The initial documentation of competitive hierarchies among forest trees in North America was presented by Baker (1949) in which species were assigned, by consensus among foresters, to one of five tolerance classes. This is consistent with Tilman's (1982) proposal that the competitive dominant in a habitat is the species able to produce and tolerate the lowest levels of a limiting resource, in this case light. While the tolerance ratings summarize the general pattern, the tolerance of a species may vary with climate, local site conditions, associated species, vegetative condition (seedling or sprout), and age (Spurr and Barnes 1980). But within local regions (e.g. the Great Lakes – St. Lawrence Forest Region) the relative tolerance among species appears to be constant.

The usual tolerance values for tree species occurring in the Alaskan taiga and the Great Lakes St. Lawrence Forest Region are listed by tolerance class in Table 1 (Baker 1949, Fowells 1965). Two other tolerance ratings for the Great Lakes–St. Lawrence species (Graham 1954, Horton and Brown 1960) are also included. There is apparent concordance among all three rating systems, although they are not strictly independent schemes.

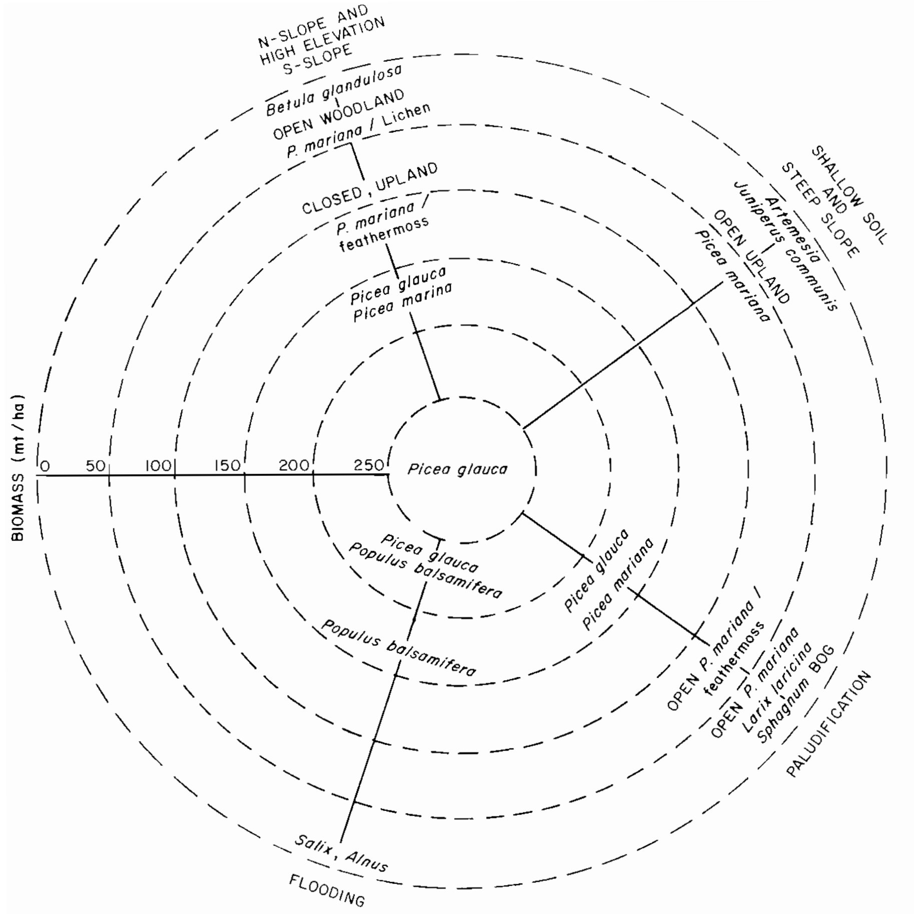

Fig. 2. Centrifugal organization of forest ecosystems in the Alaskan taiga. (Data from Van Cleve et al. 1986)

The mechanisms of shade tolerance are unimportant for the purposes of evaluating whether competitive hierarchies occur. However, research has shown that shade tolerance is not only the result of an ability to utilize low levels of light, but is more precisely the ability to be competitively superior in securing moisture and nutrients under low light levels (Kimmins 1987). Shade intolerant species may have specific physiological traits to regenerate in gaps (Spurr and Barnes 1980, Smith 1982), but others, according to Spur and Barnes (1980: 382), have "adaptation to extreme site conditions. They are typically adapted to some type of xeric (warm or cold) or infertile site as well as to the climatically extreme, initial conditions of the disturbed site. Thus they may form relatively permanent communities on extreme sites where more tolerant species are at a disadvantage."

This is in agreement with a central assumption of the centrifugal organization of a set of species (Rosenzweig: 1987:179) "Though all species should be able to thrive in an environment free of all types of stress, each may need to specialize on the type of stress it can most efficaciously withstand."

The competitive hierarchy based on shade tolerance is now used throughout the forestry literature as a basis of comparison among species for forest management (see Fowells 1965), for species replacement models (Horn 1971, 1981, Houston and Smith 1987) and is also used in forest growth models as a parameter for growth in relation to shading (Shugart and West 1977, Shugart 1984). It is especially useful in gap phase models for assigning trees to either a shade tolerant or shade intolerant photosynthetic response curve, with most North American models using Baker's (1949) tolerance ratings (Shugart 1984). In some instances authors have opted for the use of a three class shade tolerance rating system (tolerant, intermediate, intolerant) (Bormann and Likens 1979), which is based on similar distinctions of the competitive ability among the species. At the global scale, Box (1981) has produced a general model for predicting vegetation types in different climates. A key component is hierarchies of dominance, where, once a subset of species which can tolerate the local climate is selected, large growth forms exclude smaller ones.

We therefore conclude that the existing paradigm in forestry is consistent with the competitive hierarchies

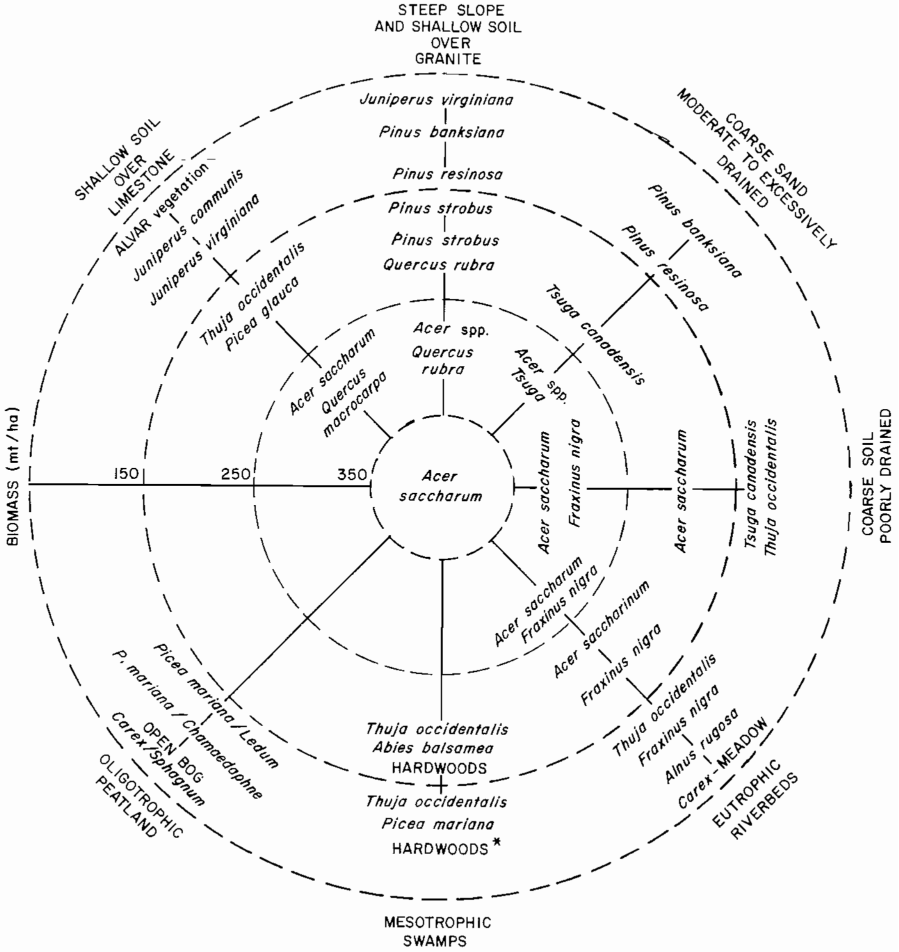

Fig. 3. Centrifugal organization of forest ecosystems in the Great Lakes–St. Lawrence Forest Region. Other species which may share dominance with *Acer saccharum* in the core habitat are *Fagus grandifolia, Betula alleghaniensis,* and *Tilia americana.* (*HARDWOODS include *Ulmus americana, Fraxinus americana, F. nigra, Acer saccharum* and *A. rubrum*). (Data from Maycock and Curtis 1960, Maycock 1963, Auclair and Goff 1971, Rowe 1972, Catling et al. 1975, Gagnon and Bouchard 1981, Pregitzer and Barnes 1984, Spies and Barnes 1985, Domon et al. 1986) (Biomass estimates from Reiners 1972, Whittaker et al. 1974, Crow 1978, Kimmins et al. 1985)

described from herbaceous vegetation. We next explore whether the patterns of species distributions along environmental gradients are consistent with those in temperate wetlands.

Centrifugal organization models

Alaskan taiga ecosystems

A centrifugal model of the patterns in forest community types in interior Alaska (Van Cleve et al. 1986) is illustrated in Fig. 2. The mesic, most-fertile sites (south slopes and floodplains) in the core of the model are dominated by *Picea glauca* (Moench) Voss, the most shade tolerant species within the species pool. These sites have also been relatively undisturbed for the past 100 to 200 yr. Radiating from this core community type are constraint gradients of slope, aspect, altitude, mineral soil depth, organic matter depth, and disturbance. *Picea mariana* (Mill.) B. S. P. is the dominant species on oligotrophic sites whether they are xeric on shallow, north exposures or hydric sites on peatland. Changes in

Table 1. Shade tolerance ratings of tree species of the Great Lakes St. Lawrence Forest Region and the Alaskan taiga.

	Baker (1949) Fowells (1965)	Graham (1954)	Horton and Brown (1960)
Very tolerant	*Tsuga canadensis*	10.0	4
	Abies balsamea	9.8	1
	Acer saccharum	9.7	2
	Fagus grandifolia		3
Tolerant	*Tilia americana*	8.2	
	Picea glauca	6.8	5
	P. mariana	6.4	8
	Acer rubrum	5.9	11
	Thuja occidentalis	5.0	
Intermediate	*Betula alleghaniensis*	6.3	6
	Pinus strobus	4.4	7
	Fraxinus nigra	2.4	
	Quercus rubra		10
Intolerant	*Pinus resinosa*	2.4	12
	Prunus serotina	2.4	
	Pinus banksiana	1.8	13
	Betula papyrifera	1.0	9
Very intolerant	*Larix laricina*	0.8	
	Populus grandidentata	0.7	15
	P. tremuloides	0.7	14
	Prunus pensylvanica		16

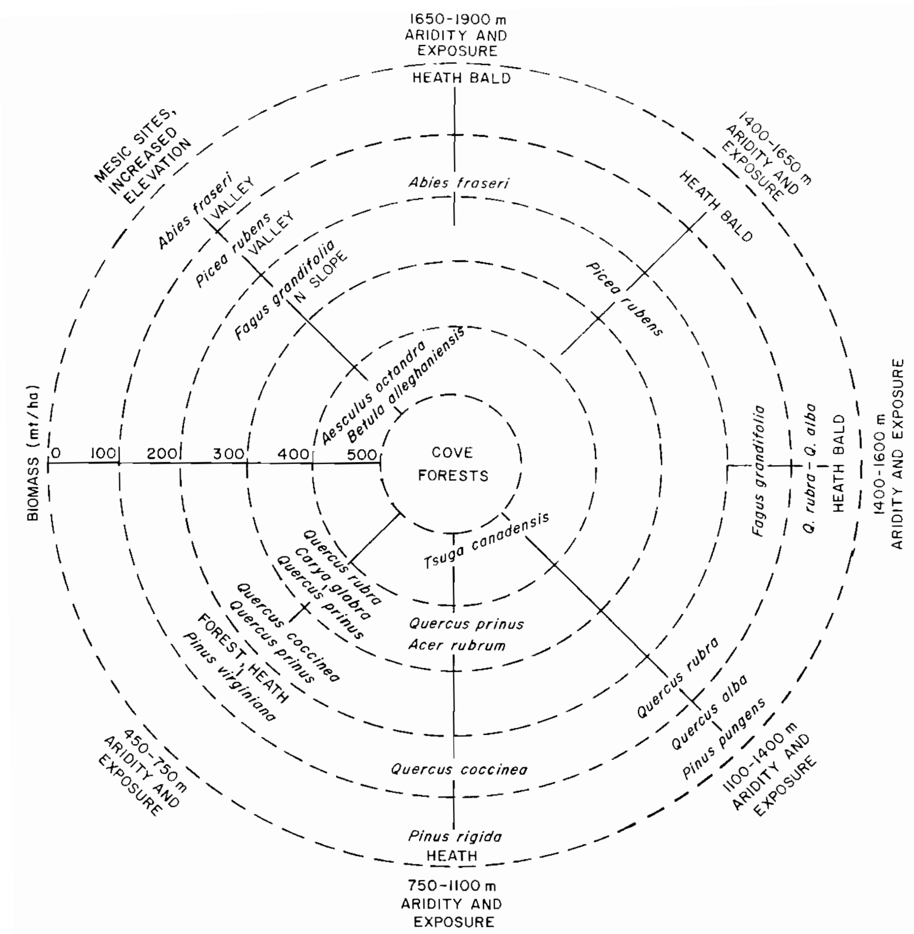

Fig. 4. Centrifugal organization of upland forest communities of the Great Smoky Mountains. Species which share dominance in the cove forests include *Acer saccharum, Aesculus octandra, Betula alleghaniensis, Halesia carolina, Tilia heterophylla,* and *Tsuga canadensis. Fagus grandifolia* and *Liriodendron tulipifera* are also important in some of the stands of the cove forests.
(Data from Whittaker 1956, Woods and Shanks 1959, Whittaker et al. 1966, Golden 1981.)

time, which are either autogenic (paludification), or allogenic (flooding) create extreme site types, characterized by shade intolerant species, around the periphery. The whole model is scaled on above ground tree biomass, which decreases from the core community to the peripheral communities.

Great Lakes–St. Lawrence forest region

Acer saccharum Marsh. is the dominant core species on mesic, fertile sites within the Great Lakes–St. Lawrence Forest Region (Maycock 1963) (Fig. 3). It may, on occasion, share this dominance with other hardwoods such as *Tilia americana* L., *Fagus grandifolia* Ehrh., and *Betula alleghaniensis* Britton (Rowe 1972). *Acer saccharum, Tilia americana* and *Fagus grandifolia* are classified as very tolerant and tolerant species, with *Betula alleghaniensis* being of intermediate shade tolerance (Table 1).

Stress gradients within this forest are largely related to physiography (Rowe 1972). *Pinus* species tend to dominate on xeric sites (Maycock and Curtis 1960, Gagnon and Bouchard 1981, Pregitzer and Barnes 1984, Spies and Barnes 1985). On hydric sites deciduous species are characteristic of eutrophic sites along rivers [e.g. *Fraxinus nigra* Marsh. (Pregitzer and Barnes 1984, Spies and Barnes 1985), *Acer saccharinum* L. (Domon et al. 1986)], while coniferous species (particularly *Picea mariana*) are characteristic of oligotrophic areas (Spies and Barnes 1985). *Juniperus* species tend to be confined to the most xeric sites on shallow soils over either limestone (Catling et al. 1975) or granitic bedrock (Gagnon and Bouchard 1981).

As soil conditions become more unsuitable for plant growth towards the periphery, *Acer saccharum* maintains its presence, but not its dominance. It becomes a co-dominant with *Fraxinus nigra* and *Tsuga canadensis* (L.) Carr. on poorly drained sites, (Spies and Barnes 1985) and with *Quercus rubra* L. on more xeric sites (Gagnon and Bouchard 1981, Pregitzer and Barnes 1984, Spies and Barnes 1985). However it does drop out completely in the more extreme sites.

These comparisons suggest that woody species have the same patterns observed in wetlands. One (or several) shade tolerant canopy-forming species occupies the most productive sites, producing high biomass communities. Gradients which radiate outward from the preferred site produce extreme site types which allow shade intolerant species to escape from the competitive dominants. One could push for limits to such generalities by exploring patterns in wetlands or forests further south. We therefore next direct attention to the extensive data on forests in the southern Appalachian Mountains (e.g. Whittaker 1956).

Great Smoky Mountains

Gradients within the Great Smoky Mountains are diverse as a result of the rapid changes in topography. As a first approximation, Whittaker's (1956) gradient analysis was aligned along a moisture gradient, from the sheltered cove forests to the exposed south-facing ridges, and also along an elevation gradient from (500 to 1800 m). Whittaker's study did not include the diverse communities present on limestone, nor the floodplain communities (Harmon et al. 1983), which represent two additional gradients within this forest system. The grassy balds (Whittaker 1956) were not included in the model, since they are generally thought to be due to anthropogenic disturbances (Lindsay and Bratton 1979).

The cove forests of the Great Smoky Mountains occupy the mesic, most fertile sites and sheltered sites, up to an elevation of 1400 m (Whittaker 1956) (Fig. 4). This represents the core habitat of the region, but rather than a single dominant as in taiga, or a prominent dominant as in the case of *Acer saccharum* in the Great Lakes St. Lawrence Forest, there are six species which share dominance within this habitat (i.e. *Aesculus octandra* Marsh., *Acer saccharum, Betula alleghaniensis, Halesia carolina* L., *Tilia heterophylla* Vent., *Tsuga canadensis*). The composition of the core habitat changes with elevation: at mid-elevations the cove forests become dominated by *Aesculus octandra* and *Betula alleghaniensis*, with many other species dropping out. At high altitudes the core habitat is dominated by *Abies fraseri* (Pursh.) Poir. The most extreme sites in regards to elevation and moisture are occupied by shade intolerant/stress tolerant evergreen species, such as coniferous trees (e.g. *Pinus rigida* Mill.) and ericaceous shrubs (*Kalmia latifolia* L.).

Discussion

Generality of centrifugal organization

The objective of this paper was to assess the generality of the centrifugal organization model. The data presented here suggest that forests, like wetlands, display the pattern and process of centrifugal organization. This is significant because we have extended generality in two directions: from aquatic to terrestrial habitats, and from herbaceous to woody plants. With hindsight, these results are not surprising, since stress and disturbance gradients, as well as competitive interactions, can be found to varying degrees in all vegetation types (e.g. Grime 1979, Tilman 1988, Keddy 1989).

While the generality is noteworthy, it is none-the-less of interest to examine lack of fit in the Great Smoky Mountains data. In such cases there are two options. One is to conclude that the model has reached the limits of applicability. The other is to explore whether some simple modifications to the model will allow it to be extended to incorporate the apparently conflicting data. One does not want to fall into the trap of simply stretching the model to accommodate all observations, but neither is it advisable to immediately conclude that a new model must be constructed for a different biome.

High alpha diversity in core habitats of southern forests

The wetland model proposed that the core habitat is dominated by a few species, with alpha diversity and gamma diversity (sensu Whittaker 1960) increasing towards the periphery. This occurs in the taiga and for the northern transition forests, but not in the southern forests. Auclair and Goff (1971), Glenn-Lewin (1977) and Peet (1978) have provided many other examples which illustrate conflicting patterns of alpha diversity along environmental gradients. Such contradictions may not mean that a centrifugal model is inappropriate, but rather that in some vegetation regions there are more mesophytic, shade tolerant species available to share the resources within the optimum core habitat. In our three examples, it appears that the number of species increases as one descends in latitude. In tropical rain forests mesic habitats may have many tree species (at least 50–150 tree species ha^{-1}, Whitmore 1982), but mesic sites can also be dominated by single species (Connell and Lowman 1989). Terborgh (1973) has presented evolutionary arguments as to why, in general, core habitats should have higher diversity than peripheral habitats, but this is clearly not true for some vegetation types such as wetlands (Fig. 1) and grasslands (Ellenberg 1988). The evolution of diversity in core habitats is an unresolved problem. We do not need to address the evolutionary issues further here, since our objective is to deal with observed patterns in diversity on ecological rather than evolutionary time scales.

The presence of shade intolerant species (e.g. *Liriodendron tulipifera* and *Betula alleghaniensis*) in core habitats in southern Appalachian forests suggests that gap disturbance is important in these forests (Runkle 1985), as in nearly all forests (Pickett and White 1985, Platt and Strong 1989). There are at least two mechanisms by which gap regeneration might maintain such

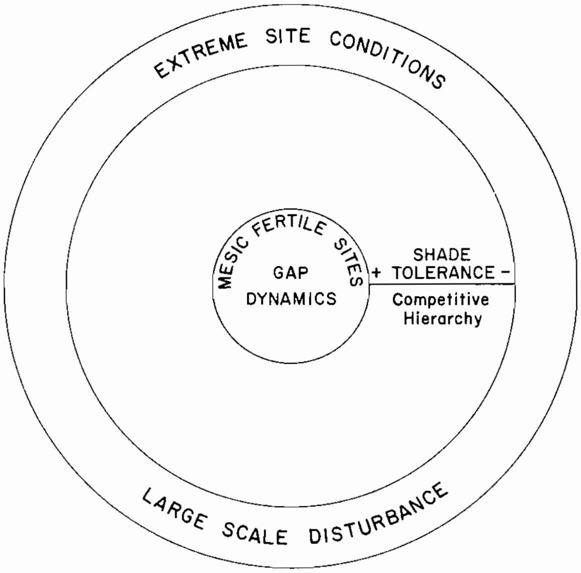

Fig. 5. Summary of mechanisms operating in the centrifugal organization model of forest communities.

diversity. The first may be that many of these species are competitive equivalents, with coexistence resulting largely from the very slow rates of competitive exclusion (e.g. Aarssen 1983, Ågren and Fagerström 1984, Hubbell and Foster 1986). A second possibility may be to invoke niche differentiation and assume that these species coexist through differences in their regeneration niche (sensu Grubb 1977); coexistence might therefore be largely a function of small scale disturbance, or gap dynamics (Runkle 1985). More generally, coexistence may be a function of a temporally varying environment and varying recruitment rates as in the lottery model (Chesson 1986).

In the core of the centrifugal model (Fig. 5) representing mesic, fertile sites, species coexistence occurs through gap dynamics. If the species pool is low enough, such as in *Typha* marshes or *Picea glauca* forests, this region is dominated by a single species which lowers light levels below the tolerance limits of all other species. At the periphery, extreme site conditions produce a range of vegetation types. Here, specialization upon different sites by species produces coexistence only at a larger, landscape scale of organization. Disturbance may occur in this region, but it is large scale disturbance associated with events such as major fires and floods. Therefore, while both the core and periphery are influenced by disturbance, these occur at different temporal and spatial scales in the two regions. Finally, in the intermediate region, species are organized along natural gradients by their decreasing levels of shade tolerance.

Some possible tests

A test of some of these proposed mechanisms could be conducted by field experiments in which species are removed from different sections of gradients and the response of other species to these removals are monitored. (One could also conduct similar experiments by creating gradients with core and peripheral habitats under experimental conditions (e.g. Sharitz and McCormick 1973, Austin and Austin 1990, Grace 1990).) For example, (1) removing a species from a core habitat would be predicted to result in increased abundance of competitive equivalents. In contrast, removing a species from an intermediate habitat would be predicted to allow competitive subordinates from the periphery to invade more fertile sites. That is, competion along these gradients should be one-sided (Keddy 1990) unless competitive equivalents exist to increase and maintain the canopy and lower light levels. In sites dominated by a single species, removal of the canopy should lead to invasion by species from lower biomass sites. (2) In peripheral habitats, removal of a species should generally not allow other woody species to invade, but rather lead to a shrub or herb dominated community. (3) Transplant experiments could test whether inclusive niche structure (sensu Miller 1967, Colwell and Fuentes 1975) and competitive hierarchies are indeed producing the observed distribution patterns along natural gradients.

A second approach would be to compare plant traits across many species simultaneously, using species from a range of habitats. Traits providing tolerance to low productivity (e.g. shallow soil, drought, flooding) should be negatively correlated with tolerance to shading.

A third approach would be to examine state variables such as total species pool in other northern temperate forests. The prediction is that the species pool of woody plants should decrease with increasing biomass.

A natural experiment

One test of these predictions might come from the natural removal experiment resulting from the eradication of *Castanea dentata* (Marsh.) Borkh. by the chestnut blight (*Endothia parasitica* (Murr.)). *Castanea dentata* was still a recognizable dominant within the Great Smoky Mountains at the time of Whittaker's (1956) study, but since that time the *Castanea* has been replaced. In the sub-mesic sites where *Castanea* occurred in the cove transition forests, replacement in *Castanea* gaps was by shade tolerant, mesophytic species, primarily *Tsuga canadensis* and *Halesia carolina* (Woods and Shanks 1959). In sub-xeric sites, *Castanea* was replaced by its co-dominants, *Quercus prinus* L., and *Quercus rubra* L., (of equivalent shade tolerance) along with *Acer rubrum* L. Both these situations appear to represent changes attributable to replacement by competitive equivalents which were co-dominants at these sites. However, in the xeric areas where *Castanea* occurred (dry slopes and ridges), it was replaced by more shade intolerant, xerophytic species (*Quercus coccinea* Wang. and *Pinus rigida*). Replacement by species from more marginal sites rather than from the core sites is consistent with the predictions of the centrifugal organization model.

Conclusions

We conclude that competitive hierarchies structure forests, and that the patterns of species distributions in forests are largely consistent with the centrifugal organization model developed for herbaceous wetland vegetation. We have speculated that in forests, gap dynamics in the core habitat is more important, leading to different patterns in species richness, particularly at lower latitudes. Additional tests are needed to explore both the generality of the patterns of centrifugal organization, and the role of competition as an important underlying mechanism.

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