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LIMITING SIMILARITY IN MECHANISTIC AND SPATIAL MODELS OF PLANT COMPETITION IN HETEROGENEOUS ENVIRONMENTS

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Abstract.—We study two kinds of mechanistic and spatial models of plant competition in heterogeneous environments. First, we study lottery models in which the outcome of competition among juveniles for vacant space is determined by one of several underlying mechanistic sub-models. Environmental heterogeneity that affects the outcome of competition is present in all of these models and may be spatial, temporal, biotic in origin, abiotic in origin, or any mixture of these. The principal result is that the models predict coexistence if the plant species are sufficiently dissimilar—if they sufficiently partition the spatial, temporal, biotic, or abiotic environmental heterogeneity. Second, we study a complex forest-simulation model of competition among individuals for light and a nutrient. Whereas the nonspatial version of this model predicts that a single species will outcompete all others, the spatial version predicts that coexistence is possible. We show that the results for the analytically tractable models appear to explain the cause and pattern of coexistence in the simulation model.

Over the past decade, a variety of population dynamic models have been developed that include fundamental characteristics of plants (reviewed in Roughgarden 1987; Pacala 1989). Several of these treat competition as a phenomenological density-dependent process and include spatial and temporal environmental heterogeneity (see, e.g., Shmida and Ellner 1984; Chesson 1985; Pacala and Silander 1985, 1990; Crawley and May 1987; Pacala and Crawley 1992). Simple mechanistic (resource-based) models of competition between plant species have been studied extensively by Tilman (1982, 1985, 1988). Mechanistic models expose the costs associated with a nonmechanistic approach—that it is difficult to deduce how the parameters of a phenomenological competition model map to readily observable attributes of plants and their environment. For example, competition coefficients in a phenomenological model will depend on resource availability, as well as morphological and physiological attributes of plants. There is simply no obvious way to determine how these coefficients vary from place to place and among species unless the phenomenological model is itself based on some mechanistic understanding of competition. Thus, the predictions of mechanistic models are often more easily interpreted than the predictions of phenomenological models.

An alternative to simple mechanistic or phenomenological modeling has been to simulate the birth, dispersal, growth, and death of each individual in a popula-

tion with a computer (see the review in Shugart 1984). Typically, computer simulators include the mechanism of competition, with taller plants shading smaller plants and all plants competing for water and nutrients. Computer simulators have been designed primarily to mimic the dynamics of specific plant communities (usually forests). However, Tilman (1988) has recently used a computer simulator closely related to forest models such as FORET (Shugart and West 1977) to explore possible causes of patterns in successional vegetation. In Tilman's (1988) model, plant species are drawn from a "universe of possible species" representing all possible static allocation strategies of photosynthate to leaf, stem, and roots. The model predicts how the strategies of dominant plant species change during succession and along environmental gradients.

In this article we study simple spatial and mechanistic models of plant communities inhabiting spatially and temporally variable environments. The models are similar to spatial "lottery" models in that plant species compete for the possession of spatial cells made vacant by disturbance (see, e.g., Hastings 1980; Shmida and Ellner 1984; Comins and Nobel 1985; Warner and Chesson 1985; Pacala and Crawley 1992). Throughout, we draw extensively on Chesson's (1983, 1984, 1985, 1986) mathematical criteria for coexistence in heterogeneous environments. Unlike previous lottery models, the outcome of competition is determined by an underlying mechanistic model of competition. Our approach is sufficiently general to permit a wide variety of underlying mechanistic models, including competition for light, water, and nutrients as affected by predators, pathogens, and mutualists.

Following Tilman (1988) we also construct universes of possible plant species that specify the competitive strategies of plants and functional trade-offs inherent in these. We consider a series of cases intended to illustrate a range of possible trade-offs that may be important in natural communities. For example, we consider cases in which: (1) species compete for a single limiting resource, plant performance is temperature sensitive, and species differ only in optimal temperature; (2) species compete for light and a soil nutrient and differ only in allocation to root, stem, and leaves (or simply root and leaves)—this case focuses on the trade-off between aboveground and belowground resource acquisition; (3) species compete for a single resource but are also affected by herbivory—low palatability implies low photosynthetic efficiency and high palatability implies high photosynthetic efficiency.

Our most significant finding is that environmental heterogeneity leads to the existence of limiting similarities among coexisting plant species. These limiting similarities are minimum spacings between the strategies of species that must be exceeded for the species to coexist. For example, coexisting species must have sufficiently different optimal temperatures in case 1, root-shoot ratios in case 2, and palatabilities in case 3.

In all cases that we consider, coexistence and limiting similarities result because of interspecific variation in competitive abilities *during replacement*. Thus, our model is one possible formalization of "regeneration niche" theory as discussed extensively by Grubb (1977, 1986) and more recently by Chesson and Huntly (1988, 1989). We emphasize that our results require spatial and/or temporal heterogeneity. In contrast, the principal results from the widely studied niche-

theoretic models introduced by MacArthur (MacArthur 1972; Bulmer 1974; Roughgarden 1976; Christiansen and Fenchel 1977; Mattessi and Jayakar 1980, 1981; Slatkin 1980; Case 1982; Pacala and Roughgarden 1982; Milligan 1985; Rummel and Roughgarden 1985; Taper and Case 1985; Pacala 1988; Chesson 1990) do not require spatial or temporal heterogeneity. Species coexist in MacArthur's model by feeding on different kinds of prey.

The explanation of coexistence in our model is simple. A species will persist in the following cases: (1) there are at least some places and/or times in which it is a stronger competitor during regeneration than all other species present, or (2) the species is sufficiently capable of sending propagules from one such place or time to another. This second requirement for persistence implies that diversity is recruitment limited in the model in the same way that abundance may be recruitment limited in models of intertidal organisms (Roughgarden et al. 1985, 1988).

In what follows, we first introduce some mechanistic models of competition during regeneration and integrate these into the spatial lottery model. We then show how environmental heterogeneity leads to coexistence and limiting similarity. Finally, we introduce a complex spatial simulation model of mechanistic competition among plants (a spatial version of the model in Tilman 1988). We do not attempt a complete analysis of the simulator but rather show, with a limited number of runs, that the results from the simple analytically tractable models are, at least in these cases, robust to the added complexities in the simulator. Specifically, we demonstrate that species in the simulation model coexist if they sufficiently partition the spatial and temporal heterogeneity in light and nutrient levels created by the plants themselves.

EXAMPLES OF MECHANISTIC MODELS

Here we present three mechanistic models of competition among plant species. This collection is intended solely to illustrate the range of processes to which our results apply and is specifically not intended as an exhaustive list of important mechanisms. In what follows, we refer to the mechanistic models as *submodels* to distinguish them from the mechanistically based lottery models that we construct with them.

In each mechanistic submodel, we assume that there is a single axis along which the environment may vary and a single axis along which species are differentiated (the universe of possible species). We construct the submodels so that a single species inevitably excludes all others in a homogeneous environment. The identity of the dominant species, however, is different in different environments. We define the optimal environment, or "niche position," for each species as the single environmental condition in which it is a stronger competitor *than any other conceivable species* (in the universe of possible species). We then derive the set of environmental conditions in which each species is a stronger competitor than the other species in its habitat. This set obviously contains the species' niche position. We also show that the set contains only those environmental conditions that are, in some sense, closer to the species' niche position than to the niche position of any other species present.

Submodel 1: temperature-dependent performance.—Consider Tilman's (1980) simple model of competition for a single limiting nutrient:

$$\begin{aligned}\frac{dB_i}{dt} &= B_i(G_i(R) - d_i); \\ \frac{dR}{dt} &= S - aR - \sum_{i=1}^Q w_i B_i G_i(R).\end{aligned}\quad (1)$$

Here, B_i is the biomass of the i th plant species, $G_i(R)$ is the net rate of production of new biomass, and d_i is the death rate. Production depends on the availability of the limiting nutrient R . The dynamics of the resource are determined by its supply rate (S), leaching rate (a), and consumption by plants. The consumption is simply the sum, over all plant species, of the concentration of resource in tissues of the i th plant species (w_i) times the production of new biomass of that species.

As Tilman (1982) shows, this model predicts that a single species will outcompete all others. The winning species is the one that, in monoculture, would drive equilibrium nutrient concentration (R^*) to the lowest level.

It is widely known that production rates depend on temperature. Net photosynthetic rates are typically highest at a single temperature and decline to either side of this optimum. Also, thermal optima differ markedly among species (see, e.g., Gates 1969). To add temperature-dependent production to equations (1), we write net production as $G(R, T|T_i^*)$, where T is the temperature of the habitat and T_i^* is the thermal optimum for species i . For simplicity, we assume that species are identical except for their thermal optima (to avoid a problem involving multidimensional niches). Then, the optimum T_i^* is the niche position of species i and the universe of possible species is the range of possible values of T_i^* .

With these modifications, the model still predicts that the species that furthest reduces equilibrium nutrient concentration will exclude all others. But now, the identity of this species depends on temperature in a simple way. It is easily shown that the dominant competitor is the species whose optimal temperature (niche position) is, in some sense, closest to the environmental temperature (T). Specifically, if we label the species such that $T_1^* < T_2^* < \dots < T_Q^*$, then species i will be the dominant competitor whenever T is greater than a threshold between T_{i-1}^* and T_i^* and less than a threshold between T_i^* and T_{i+1}^* . Thus, the identity of the competitive dominant will change from place to place and time to time because of changes in temperature.

Submodel 2: root-shoot allocation.—Consider a forest in which juveniles compete for vacant gaps. In the spirit of Tilman's (1982) models, we assume that the relative growth rate of a sapling of species i is the minimum of its rates of light- and nutrient-limited production:

$$\left[\begin{array}{c} \text{relative} \\ \text{growth rate of} \\ \text{a species } i \\ \text{plant} \end{array} \right] = \text{MIN} \left[\begin{array}{c} A_i f_L(L) - r \\ (C - A_i) f_R(R) - r \end{array} \right]. \quad (2)$$

Here A_i is the fraction of species i biomass that is leaves, $f_L(L)$ is the light-limited production rate (per unit of leaf biomass), r is the respiration rate, $C - A_i$ is the fraction of species i biomass that is root ($1 - C$ is the stem fraction), and $f_R(R)$ is the nutrient-limited production rate (per unit of root biomass). Notice that species are assumed to differ only in their allocation strategies.

The competitive abilities of the saplings depend on the local availability of light and nutrient. For simplicity, the functions $f_L(L)$ and $f_R(R)$ are assumed to be monotonically increasing functions (restricting the submodel to cases involving no supersaturation of photosynthesis or nutrient toxicity), and so we may substitute $f_L(L)$ for L as a measure of light availability and $f_R(R)$ for R as a measure of nutrient availability. Further, we define the ratio of availabilities $f_L(L)/f_R(R)$ as V . We say that species i 's growth rate is "optimal" for resource levels L and R if its allocation strategy, A_i , confers a higher growth rate at these resource levels than would any other allocation strategy. Species i 's growth rate is, in this sense, optimal if its light-limited and nutrient-limited production rates are equal: $A_i f_L(L) = (C - A_i) f_R(R)$, which reduces to $f_L(L)/f_R(R) = (C/A_i - 1)$. Thus, the optimal resource ratio or niche position of species i , V_i^* , is equal to $C/A_i - 1$. A species may be characterized by its value of V_i^* (range from zero to infinity).

Light and nutrient levels in natural gaps are determined by a host of factors, including shading and nutrient uptake of surrounding vegetation, soil type, the litter chemistry of the adult that died when the gap was created, and resource use by saplings. For simplicity, we assume that resource uptake and shading by saplings do not significantly affect the resource levels that determine the identity of the winning sapling. This assumption might be appropriate, for example, if (1) saplings are too small to significantly affect resource levels immediately after a gap is formed, (2) differences among initial growth rates lead to deterministic interspecific variation in size by the time that competition among saplings becomes important, and (3) the deterministic differences in size are subsequently amplified by intersapling competition (see Ross and Harper 1972) that determines the winner of the gap. Thus, we use the optimal resource ratios defined above to determine which species captures a gap.

Just as the strongest competitor in submodel 1 is the species whose optimal temperature T_i^* is, in some sense, closest to the environmental temperature T , so the strongest competitor in submodel 2 is the species whose optimal resource ratio V_i^* is "closest" to the resource ratio in the contested gap (V). We again label the species in order of their niche positions: $V_1^* < V_2^* < \dots < V_Q^*$. It is easy to prove that species i will be the fastest-growing species if V is in an interval whose lower bound is greater than V_{i-1}^* and whose upper bound is less than V_{i+1}^* . Thus, the species identity of the dominant competitor will vary among gaps because of spatial or temporal variation in resource ratios.

Submodel 3: a trade-off between palatability and competitive ability.—Suppose that plant species compete for a single limiting resource and are also consumed by a generalist herbivore. Species differ in palatability and we assume that production efficiency increases with palatability. We are aware that there exist few data that unambiguously demonstrate the proposed relationship (see Crawley and Pacala 1991), and we assume it here merely to illustrate how plant-animal interactions can be integrated into a niche theory of plant competition.

Again using Tilman's (1980) model of competition for a single limiting resource, we have

$$\begin{aligned}\frac{dB_i}{dt} &= B_i[G_i(R) - d_i - q_i H]; \\ \frac{dR}{dt} &= S - aR - \sum_{i=1}^Q w_i B_i G_i(R),\end{aligned}\quad (3)$$

where H is the local abundance of the herbivore, q_i is both the slope of the herbivore's linear functional response and our measure of palatability, and other terms are as defined in submodel 1. To include the positive relationship between palatability and production efficiency, we now write the production rate, $G_i(R)$, as the product of two terms: $G_i(R) = N(q_i)f(R)$, where $N(\cdot)$ is an increasing function of palatability and $f(\cdot)$ is an increasing function of resource availability. Note that the plant species are identical in every way except palatability (q_i). For simplicity, we do not include explicit dynamics for the herbivore but rather assume that H is a parameter determined by factors other than the local abundances of the plant species and that H may vary from time to time or place to place. Thus, H is an environmentally variable parameter analogous to T in submodel 1 or V in submodel 2.

As in submodel 1, the plant species that furthest reduces equilibrium resource availability (R^*) will competitively exclude all others. Because $f(R)$ is an increasing function, we may use $f(R^*)$ interchangeably with R^* as a measure of equilibrium resource availability. The equilibrium availability in a monoculture of species i is found by setting the right-hand side of equation (3) equal to zero and rearranging to produce

$$f(R^*) = \frac{d + q_i H}{N(q_i)}. \quad (4)$$

To determine the optimal level of palatability (the level that minimizes R^*), we differentiate $f(R^*)$ with respect to q_i , set the result equal to zero, and rearrange:

$$H = \frac{dN'(q_i)}{N(q_i) - N'(q_i)q_i}, \quad (5)$$

where $N'(q_i)$ is the derivative of N with respect to q_i . The herbivore abundance given by equation (5) is niche position of species i , which we now label H_i^* , and the universe of possible species is the range of possible values of H_i^* . If herbivore abundance is at the level given in equation (5), then the strongest conceivable competitor is one with palatability q_i and thus niche position H_i^* .

In equation (4), the equilibrium availability, $f(R^*)$, is a linear function of H with nonnegative slope and an intercept that is a decreasing function of q_i . Because of these attributes, any group of plant species can be graphed as a set of intersecting lines like those in figure 1. The competitive dominant clearly changes with the level of herbivory because the *line* in the figure yielding the lowest value of f changes with H . Now, consider only those species that are sometimes dominant—those species whose f 's are lower than the f 's of all other species in the

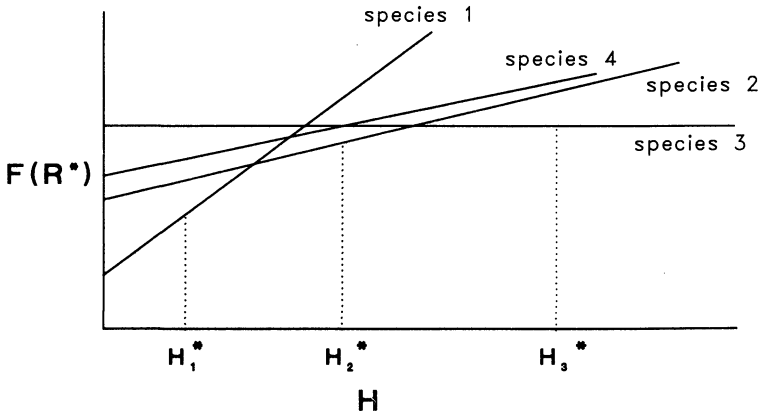


FIG. 1.—The relationship between equilibrium resource abundance in monoculture ($f(R^*)$) and herbivore abundance in submodel 3 for four plant species. A species is the strongest competitor over the range of herbivore abundances for which its $f(R^*)$ line is lower than the lines of the other species. The H_i^* are the niche positions of the plant species. Note that species 4 is never the strongest competitor.

community for some nonempty range of H . Because the range of H over which each such species is dominant must contain the species' niche position, we have a result similar to those predicated by the previous two submodels. The strongest competitor in submodel 3 is the species whose niche position (H_i^*) is in some sense closest to H , the local abundance of the herbivore during the competition. The identity of the strongest competitor will track spatial and temporal changes in the abundance of the herbivore.

MECHANISTIC LOTTERY MODELS

Perhaps the simplest and most widely studied class of spatial models of competition is the class of "discrete-cell" models introduced by Skellam (1951). The environment consists of an infinite collection of spatial cells that can contain, at most, one adult. Competition occurs only among the juveniles that occupy a cell made vacant by the death of an adult. If there are Q plant species, then

$$\Delta X_i = -d_i X_i + \sum_{j=1}^Q d_j X_j M_{ij} + \left(1 - \sum_{j=1}^Q X_j\right) M_{iF} \quad (6)$$

$\left(\begin{array}{l} \text{species } i \\ \text{change} \end{array} = \begin{array}{l} \text{death} \\ \text{capture of} \\ \text{cells just} \\ \text{vacated} \end{array} + \begin{array}{l} \text{capture of cells} \\ \text{unoccupied but not} \\ \text{just vacated} \end{array} \right),$

where X_i is the fraction of space occupied by species i at time t , d_i is species i 's adult death rate, ΔX is the fraction of space occupied at time $t + 1$ minus the fraction occupied at time t (the rate of change), M_{ij} is the probability that a species i juvenile captures a cell made vacant by the death of a species j adult, and M_{iF}

is the probability that species i captures one of the fraction $(1 - \sum X_j)$ of unoccupied cells that were vacated prior to time t .

Here, we use the mechanistic submodels of competition and simple descriptions of fecundity, germination, and dispersal to develop expressions for the M_{ij} . Beginning with the simplest case, suppose that dispersal is infinite and so there is a Poisson distribution of juveniles per cell. Also, let F be the effective fecundity of an adult plant (number of seeds produced times germination probability times probability of survival to the stage at which juveniles compete). Finally, consider the environmentally variable parameters of the mechanistic submodels that determine the outcome of competition among juveniles. We assume that these vary as independent and identically distributed random variables both from cell to cell and from time to time within the same cell.

Now, suppose that we choose one of the mechanistic submodels and let the environmentally variable parameter in this submodel be labeled E . Also, let E_i^* be the niche position of species i and let Φ_i be the set of values of E for which species i is the strongest competitor. The probability that environmental conditions in a randomly chosen cell are contained by Φ_i is thus $P_i = \int_{\Phi_i} B(e) de$, where $B(e)$ is the probability density of E and the Φ_i under the integral sign indicates that the integration is over the set Φ_i .

As in MacArthur and Levins's classic (1969) article on limiting similarity, we suppose that two codominant resident species are invaded by a third with a niche position between those of the residents. The equations governing the residents are

$$\begin{aligned} \Delta X_1 &= -dX_1 + [d(X_1 + X_2) + (1 - X_1 - X_2)][P_1(1 - Z_1) + P_2Z_2(1 - Z_1)]; \\ \Delta X_2 &= -dX_2 + [d(X_1 + X_2) + (1 - X_1 - X_2)][P_2(1 - Z_2) + P_1Z_1(1 - Z_2)] \\ &\left(\begin{array}{l} \text{change of} \\ \text{species } i \end{array} = [\text{death}] + [\text{vacant space}] \left[\begin{array}{cc} \text{fraction captured} & \text{fraction captured} \\ \text{because species } i & \text{because dominant} \\ \text{is competitively} & \text{competitor is} \\ \text{dominant} & \text{absent} \end{array} \right] \right), \end{aligned} \quad (7)$$

where Z_i is equal to the probability that no juveniles of species i are in a cell. Because of the assumption of large dispersal, Z_i is the zero term of a Poisson distribution with mean $X_i F$: $Z_i = e^{-X_i F}$. The second term in square brackets is the total probability that species i captures a randomly chosen vacant cell. This probability is the sum of two terms. The first, $P_i(1 - Z_i)$, gives the probability that the cell's environment makes species i the strongest competitor times the probability that the cell contains at least one viable species i juvenile. The second accounts for cells captured by species i only because the stronger competitor (the other species) is absent.

Although it is not possible to obtain an equilibrium solution from equation (7) in closed form, there exists an accurate and biologically reasonable approximation. In most plant communities, several juveniles compete for each vacant location, and so we expect that F is typically $\gg 1$. In what follows, we assume that

e^{-FX} is of negligible magnitude providing that $X \gg 1/F$. We thus assume that common species are never recruitment limited; juveniles of common plant species are present in virtually every disturbed cell. Plant species that occupy a sizable fraction of the total occupied space at equilibrium will have abundances that greatly exceed $1/F$ if $F \gg 1$, because it is possible to show that the total fraction of cells occupied at equilibrium ($X_1 + X_2$) is approximately $1 - O(e^{-F})$, where $O(e^{-F})$ means of order e^{-F} .

With these assumptions, the equilibrium abundances given by equation (7) are simply $X_1^* = P_1$ and $X_2^* = P_2 = 1 - P_1$. It is straightforward to prove that this equilibrium is globally stable.

The cause of limiting similarity.—We now consider the fate of an invading species I with a niche position between E_1^* and E_2^* . The presence of this invader changes the sets of environmental conditions in which species 1 and species 2 are the strongest competitors and thus changes P_1 and P_2 . For example, suppose the invader is absent and assume by a labeling convention that the niche position of species 1 is less than that of species 2. Then, Φ_1 contains all values of E less than a threshold value between E_1^* and E_2^* , and Φ_2 contains all values greater than this threshold (fig. 2a). In contrast, if the invading species is present, then Φ_1 contains only those values of E that are less than a threshold between E_1^* and E_I^* . Similarly, Φ_2 contains only those values of E greater than a threshold between E_I^* and E_2^* (fig. 2b). In what follows, we use the lowercase p_i to designate the fraction of environments in which species i is the strongest competitor *if the invading species is present* and otherwise (as in eq. [7]) use the uppercase P_i .

Using this notation, the three species system analogous to equation (7) is

$$\begin{aligned}\Delta X_1 &= -dX_1 + \Theta(1 - Z_1)[P_1Z_1 + p_1(1 - Z_1) + O(Z_2)]; \\ \Delta X_2 &= -dX_2 + \Theta(1 - Z_2)[P_2Z_1 + p_2(1 - Z_1) + O(Z_1)]; \\ \Delta X_I &= -dX_I + \Theta(1 - Z_I)[p_I + O(Z_1) + O(Z_2)],\end{aligned}\quad (8)$$

where $O(Z_i)$ means terms of order Z_i , Θ is the fraction of space that is vacant, $d(X_1 + X_2 + X_I) + (1 - X_1 - X_2 - X_I)$, and the terms to the right of Θ give the fraction of vacant sites captured by species 1, 2, and 3, respectively. Invasion by species I succeeds if the boundary equilibrium, $X_1^* \simeq P_1$, $X_2^* \simeq P_2$, $X_I^* = 0$, is locally unstable. The eigenvalue determining stability or instability is found by differentiating the right-hand side of the final question in equation (8) with respect to X_I and then evaluating the resulting expression at the boundary equilibrium:

$$\lambda \simeq -d + dFp_I. \quad (9)$$

Note that, in writing equation (9), we have neglected terms of order e^{-FP_1} and e^{-FP_2} . From equation (9) we see that invasion succeeds if

$$p_I > \frac{1}{F}. \quad (10)$$

Condition (10) results because of the species I 's recruitment limitation near the boundary equilibrium. The condition is always met if the effective fecundity is infinite. Whenever F is finite, the invader produces relatively few progeny, simply

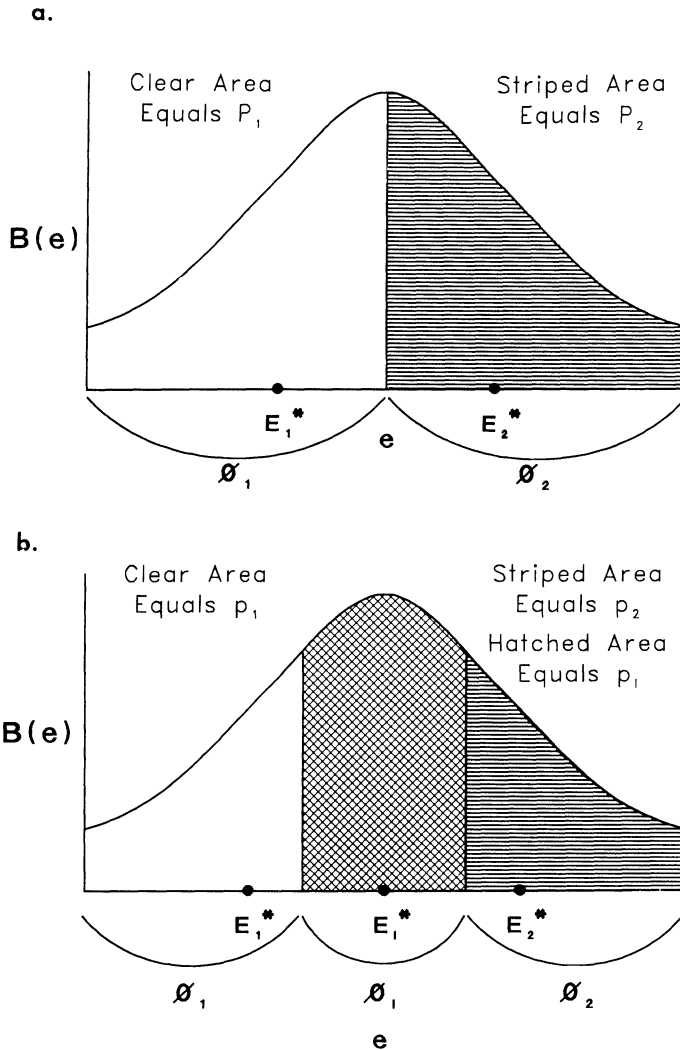


FIG. 2.—Illustration of the notation in models (7) and (8). *a*, Only the two resident species are present. *b*, The invading species and the two residents are present. Axis $B(e)$ is the distribution of the random environmental variable E , E_i^* is the niche position of species i , and Φ_i is the range of E over which species i is the strongest competitor. Note that the fraction of space or time in which each resident is dominant is different when the invader is absent (P_1 and P_2 in *a*) and present (p_1 and p_2).

because it is rare near the boundary equilibrium. Species I thus fails to colonize with its progeny some cells in which it would be the strongest competitor (cells in which E is in Φ_I). Unlike the rare invader, each common resident is not recruitment limited near the boundary equilibrium because the many adults of a common species collectively produce enough progeny to colonize virtually all cells.

Condition (10) also implies limiting similarity. As the niche positions of the

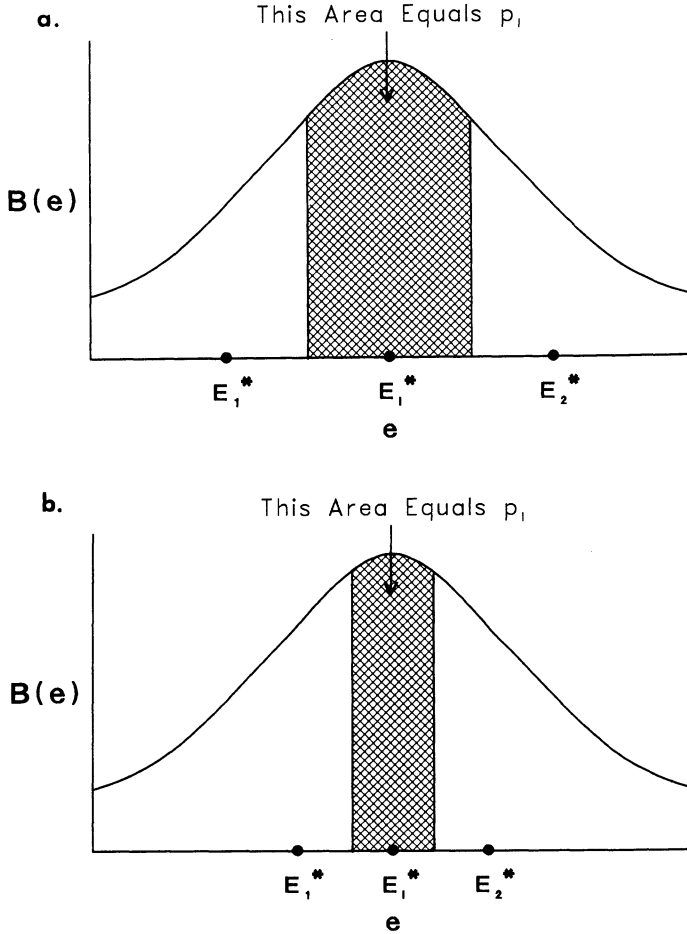


FIG. 3.—The effect of the spacing between the niche positions of the resident species (E_1^* and E_2^*) on the fraction of space or time in which the invader is dominant (p_I). Note that p_I decreases as the residents become more similar.

resident species become more similar, p_I decreases (fig. 3). The limiting similarity is the spacing between the niche positions of species 1 and species 2 that causes p_I to equal $1/F$. Thus, there is a limiting similarity between the optimal temperatures in submodel 1, between the optimal resource ratios in submodel 2, and between the optimal herbivore abundances in submodel 3. The limiting similarity in submodel 2 could be also expressed as a limit to the similarity of allocation strategies or, in submodel 3, as a limit to the similarity of palatabilities. Species I cannot invade if the resident species are too similar because places in which species I is a stronger competitor than the residents are then too rare for species I juveniles to “find” on average.

To complete the analysis of the problem, we must determine the stability of

the remaining boundary equilibria (the equilibria in which either species 1 or species 2 is absent but the others are present). If we simply relabel whichever species is absent at the boundary equilibrium as species I , then the derivation above applies and the condition for instability of the boundary remains $p_I > 1/F$. Thus, the three species coexist if the flanking species are not too similar and if the niche position of the central species is not too close to the right- or left-hand "edge" of the $B(e)$ distribution (see fig. 4).

More complex spatial models.—We now relax some of the more restrictive simplifying assumptions of models (7) and (8). First, the assumption that the environment is uncorrelated within and between gaps is clearly inappropriate in many circumstances. For example, in submodel 2, spatial variation in resource ratios caused by heterogeneous geologic parent material of soils will clearly be spatially and temporally autocorrelated. In this section, we model the environment as a series of "patches" that each contains an effectively infinite number of cells and allow the distribution of the environmentally variable parameter, $B(e)$, to vary from patch to patch. Thus, there may be interpatch variation in the mean or variance of soil fertility in submodel 2, temperature in submodel 2 (say, because of topography), or herbivore abundance in submodel 3. The important point here is that the environment may now be *spatially and temporally autocorrelated*.

Second, a variety of empirical studies show that conditions within a gap may be affected by the species identity of the former occupant. For example, interspecific differences in litter chemistry can cause nitrogen mineralization rates to be lower in gaps left by conifers than in gaps left by broad-leaved trees (Pastor et al. 1984). Similarly, populations of specialist natural enemies might be higher in a gap left by a conspecific (Janzen 1970). We thus allow the distribution of the environment in a vacant site ($B(e)$) to change with the species identity of the site's former occupant.

Third, we now include finite dispersal in a simple way. We assume that dispersal is given by a three-tiered step function. A fraction $1 - m_{Si} - m_{Li}$ of species i seeds stay within the cell in which they were produced; a fraction m_{Si} are distributed randomly (Poisson seed fall) over the entire patch of cells in which they were produced; and the remaining fraction, m_{Li} , are distributed randomly over the entire collection of patches. The subscripts S and L stand for short- and long-distance movement.

Fourth, we now decompose effective fecundity, F , into two components, a germination and establishment probability, g , and an actual fecundity, F' . Finally, we allow g , F' , and the adult death rates to vary both from species to species and from patch to patch.

In Appendix A, we derive the condition for the invasion of a species (again labeled species I) into an equilibrium community containing an arbitrary number of resident species and patches. This is formally the necessary and sufficient condition for the instability of a boundary equilibrium in which species I is absent from all patches, and the other Q species in W patches are at a locally stable equilibrium of the system of WQ equations that govern the resident community in the absence of the invader. The result is derived under the same assumptions

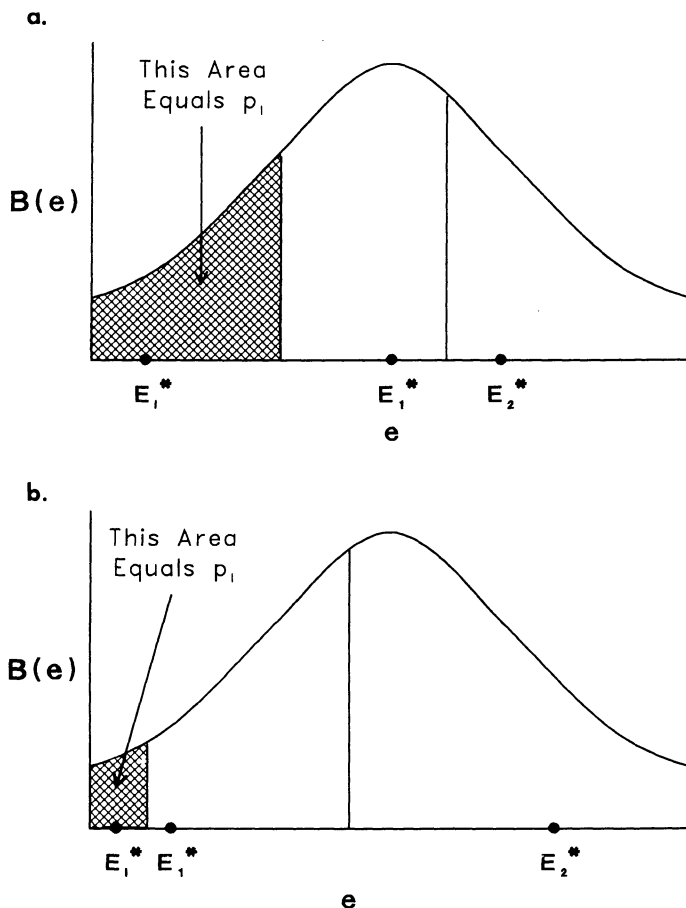


FIG. 4.—The case in which the invading species does not have a central niche position. Because the central species' niche position (E_1^*) is close to the left-hand edge of the $B(e)$ distribution in b , p_i is smaller in b than in a .

used to make the problem in the previous section analytically tractable. Specifically, all resident species are sufficiently abundant at the boundary equilibrium that none is recruitment limited. There is negligible probability that any vacant cell in any patch fails to contain a seedling of any of the resident species. We recognize that this assumption limits the generality of the result and will deal with its implications in the Discussion. It is important to remember that the invader is necessarily recruitment limited in the vicinity of the boundary equilibrium simply because it is rare when it invades.

Some additional notation is required to present the result derived in Appendix A. Let p_{ij}^k be the fraction of vacant cells in patch k that were created when a species j adult died and in which species i is the strongest competitor. In other words, $p_{ij}^k = \int_{\Phi_i} B_{kj}(e) de$, where $B_{kj}(e)$ is the distribution of E for gaps in patch

k created by the death of a species j . As before, the lower-case p signifies the presence of the invading species. Also, let g_{ik} , F'_{ik} , and d_{ik} be, respectively, the germination and establishment probability, fecundity, and adult death rate of species i in patch k . Finally, let X_{ik}^* be the fraction of cells in patch k that are occupied by the resident species i at the boundary equilibrium. Species I successfully invades if and only if either

$$b_k > 0, a_k \leq 0 \text{ or } b_k = 0, a_k < 0 \quad (11)$$

for at least one patch $k = (1, 2, \dots, W)$, or condition (11) is untrue *and*

$$\sum_{k=1}^W b_k/a_k > 1, \quad (12)$$

where $a_k = d_{Ik}(1 - p_{II}^k u_k) - \sum_{j=1}^Q d_{jk} X_{jk} p_{Ij}^k g_{Ik} F'_{Ik} m_{SI}$, $b_k = \sum_{j=1}^Q d_{jk} X_{jk} p_{Ij}^k g_{Ik} F'_{Ik} m_{LI}$, $u_k = 1 - [(1 - m_{SI} - m_{LI})(1 - g_{Ik}) + (m_{SI} + m_{LI})]F'_{Ik}$, and we adopt the convention that $b_k/a_k = 0$ if $b_k = a_k = 0$.

Condition (11) gives the condition for the successful invasion of a *patch* if it were to receive no dispersers from other patches. This condition handles cases in which the environment is so favorable in some patch that invasion succeeds there even if seed input from other patches is ignored. In contrast, condition (12) handles the case in which immigrants are required, in every patch, to balance emigration.

We now draw three conclusions from conditions (11) and (12). First, limiting similarity is predicted by these conditions. To see this, again consider an invading species with a niche position between those of two resident species. What happens as the niche positions of the residents become more similar? The situation is now considerably more complex than that shown in figure 3 because there is now a different distribution of the environment ($aB_{kj}(e)$) for each species of dead adult (j) in each patch (k). Nonetheless, if $B_{kj}(e)$ has nonzero variance, then p_{Ij}^k declines monotonically to zero as the residents' niche positions become more similar, just as in figure 3. As a result, all p_{Ij}^k ($j = 1, 2, \dots, N$; $k = 1, 2, \dots, W$) approach zero as the residents become more similar if every $B_{kj}(e)$ has nonzero variance. As all $p_{Ij}^k > 0$, each a_k in conditions (11) and (12) approaches d_{Ik} and each b_k approaches zero. Thus, if the residents are too similar, both conditions (11) and (12) are untrue and invasion fails. None of the added complexities in the model change qualitatively the prediction of limiting similarity.

Second, while we expect limiting similarities whenever the environment is unpredictable (whenever all $B_{kj}(e)$ have nonzero variance), we can show easily that predictable environments sometimes lead to the opposite conclusion. For example, suppose that E is constant within a patch but differs from patch to patch. Then, the fraction of cells in patch k in which species I is the strongest competitor is either zero or one (for all resident species j , p_{Ij}^k equals either zero or one). If the invader's niche position is exactly equal to the value of E in at least one patch, then $p_{II}^k = 1$ and $p_{Ij}^k = 1$ ($j = 1, 2, \dots, Q$) in that patch *as long as no resident has exactly the same niche position*. If F'_{Ik} in the patch is large, then u_k will be close to one and so $a_k < 0$ and $b_k > 0$. Thus, invasion

succeeds by condition (11) and the limiting similarity is zero. The point here is simply that predictable environments can allow the coexistence of as many species as there are patches, if each species is optimal in a different patch (as in Tilman 1982).

Third, consider the special case corresponding to the simple models (eqq. [7]–[8]) but with finite dispersal. Specifically, let there be one patch ($W = 1$) and let the environment of a vacated cell be independent of the species identity of its former occupant ($p_{ij}^1 = p_{iv}^1 = p_I$ for all j and v). Also, let germination rates, fecundities, adult death rates, and movement rates be identical for all species. We may thus dispense with all species- and patch-specific subscripts in the u 's, g 's, F 's, and m 's, and conditions (11) and (12) reduce easily to a single condition:

$$p_I > 1/[u + gF'(m_S + m_I)]. \quad (13)$$

The term in the denominator of the right-hand side has a simple interpretation. It is simply the average number of cells colonized by the progeny of an adult—the average number of cells that contain at least one established juvenile produced by an adult. Thus, if an adult plant's progeny establish in 10 cells on average, then species I will invade whenever it is the strongest competitor under environmental conditions occurring in at least 1/10 of the habitat. Note that a decrease in dispersal increases the limiting similarity (by decreasing the right-hand side of eq. [13]) because it increases the recruitment limitation of the invader.

Temporally variable environments.—In the models considered thus far, E may change from time to time within any one cell, but the distribution of the environment ($B(e)$) is temporally constant. In this section we allow $B(e)$ to change from one time t to the next. Such changes could be caused by, for example, year-to-year variation in mean temperature in submodel 1, nitrogen availability in submodel 2 (say, because of rainfall), or herbivore abundance in submodel 3.

Chesson (1983, 1984, 1985, 1986) has produced a comprehensive body of theoretical work on the effects of temporal heterogeneity on community structure. Here, we add uncorrelated random temporal variation of $B(e)$ to the simple models (eqq. [7] and [8]) and use Chesson's stochastic boundedness criterion to determine the success of invasion by species I . If we again assume that the resident species are never recruitment limited, then the stochastic boundedness criterion analogous to invasion condition (10) is

$$\dot{E}[\ln(1 - d + dp_I F)] > 0, \quad (14)$$

where \dot{E} stands for expectation over the distribution of p_I (p_I is now a random variable because of the random temporal variation of $B(e)$).

Chesson (1985) has shown, generally, that conditions such as condition (14) approach conditions such as condition (10) in the limit as the adult death rate approaches zero. Formally, if d is small, $\dot{E}[\ln(1 - d + dp_I F)] \approx \dot{E}[d(1 - p_I F)] = d(\underline{p}_I F - 1)$, where \underline{p}_I is the temporal average of p_I . Through this approximation, condition (14) becomes

$$\underline{p}_I > 1/F, \quad (15)$$

which is identical in form to condition (10). Condition (15) states that invasion succeeds if the temporal average of the fraction of space in which species I is the strongest competitor (\bar{p}_I) exceeds $1/F$. Note that it applies both to situations in which environmental heterogeneity is entirely temporal (p_I fluctuates in time but always equals either zero or one) and to those with a mix of spatial and temporal heterogeneity (p_I has fractional values in some years).

Just as condition (10) implies that the invader in the simple spatial model persists as a spatial fugitive, so conditions (14) and (15) imply that the invader also may persist as a temporal fugitive that continuously “disperses” through time from one period in which the environment makes it the strongest competitor to another. This temporal “dispersal” is accomplished by the long-lived adult stage in the model, and so condition (14) is never true for an annual species ($d = 1$) if there is no spatial environmental heterogeneity (if p_I fluctuates but equals either zero or one at any one time). Shmida and Ellner (1984) show that annuals may also persist as pure temporal fugitives if they have long-lived seed.

Like condition (10), conditions (14) and (15) imply limiting similarity. As the niche positions of the two resident species become more similar, an intermediate invader’s “window” of environmental conditions in which it is the strongest competitor decreases in size (fig. 5). This reduces \bar{p}_I by reducing the size of p_I in at least some years. Species I cannot invade if the similarity of the residents has reduced \bar{p}_I to a level beneath a critical threshold. This threshold is approximately $1/F$ if d is large (condition [15]) and increases as d decreases (Chesson 1985).

LIMITING SIMILARITY IN A SPATIAL SIMULATION MODEL

In this section, we demonstrate that our results extend to a model entirely unlike the analytically tractable models discussed above. Tilman (1988) published a simulation model of competition for light and nutrients that was similar to forest simulators such as FORET (Shugart 1984) in a number of respects. His simulator included individual plants competing for light and a soil resource within a single spatial cell and kept track of each individual throughout its life. Individuals grew to a maximum height and then shifted all surplus production to seed production. Growth rate was the minimum of light- and nutrient-limited production. Taller plants shaded smaller ones, plants homogeneously depleted available nutrients and nutrients returned to the available pool through decomposition. There were both random and resource-dependent sources of mortality. Typically, plants with negative growth rates were assumed to die instantly (although qualitatively identical results were obtained if plants with negative growth rates were allowed to shrink). Seeds produced on the plot did not disperse but rather germinated there (with some probability). Finally, plant species differed only in their allocation of biomass to root, stem, and leaves.

Tilman (1988) initiated runs with a large number of species (hundreds) spanning the “universe” of possible allocation strategies. Invariably, a single species eventually excluded all others, but the identity of this species changed with the rate of random mortality (disturbance) and soil fertility. Tilman used the relationship

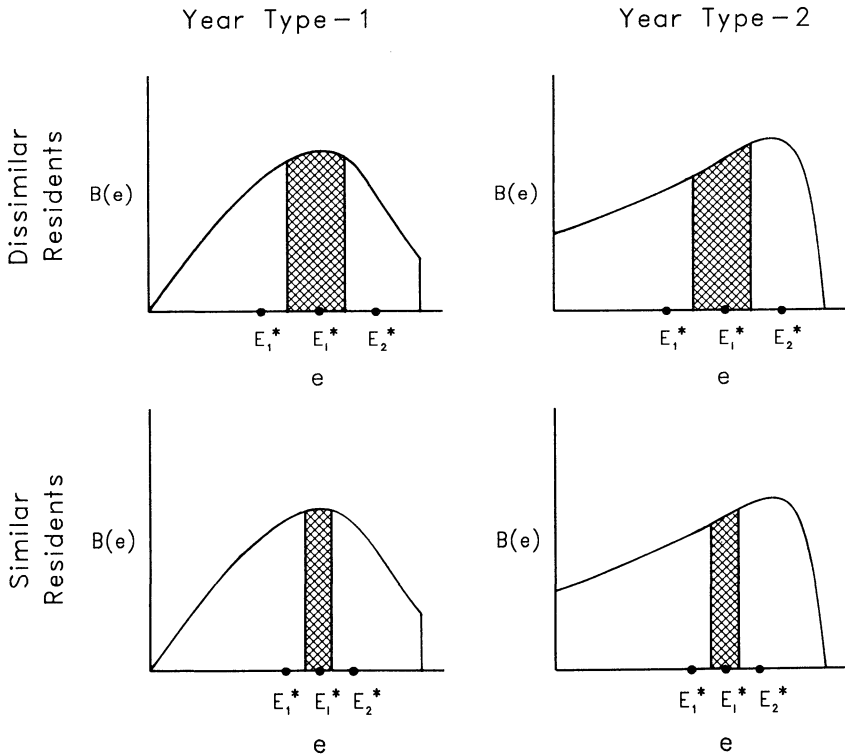


FIG. 5.—Temporal heterogeneity with two types of years. The distribution of the environmental random variable ($B(e)$) is different in the two types of years. Note that p_1 in both types of years decreases as the niche positions of the residents become more similar (cf. the upper two panels with the lower two).

between the allocation strategy of the winning species and the soil fertility or disturbance rate to explain gradients in natural vegetation.

Here, we extend this model in a simple way. Specifically, we now suppose that the environment is composed of many spatial cells. The dynamics of the cells are coupled only by seed dispersal; plants or resource levels in one cell do not directly affect those in another. The habitat is physically homogeneous in space and time, and so all environmental heterogeneity in the model is created by plants. In all examples discussed in this article, there are between 100 and 300 cells and seeds are dispersed randomly (Poisson rain) across all cells.

The problem with a complex model with unestimated parameters is that any reasonably complete exploration of the model's parameter space is impossible. Such an analysis would simply require too many runs. This problem is compounded by the enormous range of dynamical behavior typically exhibited by complex models. We did not attempt to explore completely the parameter space of our simulator. We thus have no way of assessing whether the approximately 100 simulations performed adequately represent the model's dynamical repertoire.

With this in mind, it is reasonable to ask: Why bother reporting results from the simulator at all? The answer is simply that our analytical results on limiting similarity appear to explain the outcome of competition in those simulations performed. Results from simple models are sometimes dismissed if the model used to produce them is judged to exclude too much of nature's complexity. The simulations described below suggest that our results from simple models are relevant to the simulations performed, despite the added complexities incorporated in the simulation model. Details of the simulation model and the parameter values used in all examples are found in Appendix B. Although we cannot assess the completeness of our search of the simulator's parameter space, we selected the examples in Appendix B specifically to be representative of the runs performed.

In contrast to the findings of Tilman's (1988) nonspatial model, some (approximately one-half) of the runs of the spatial simulator produced persistent communities of multiple species (see examples in fig. 6). Thus, the addition of space leads to coexistence, at least in some cases. Note, however, that the simulation model predicts relatively species-poor communities (fewer than 10 species in all runs performed). This implies that the simulation model does not include factors responsible for the observed high diversity of many natural communities (at least if our sample of runs is representative). Note also that the communities in figure 6 have qualitatively similar structure. The persistent species in each example have approximately the same allocation to stem but are spaced along a root-leaf axis. We observed this structure in all but one run that produced a persistent multispecies community. The root-leaf axis separates nutrient specialists from light specialists.

The dozens of such examples were stable equilibrium communities in the following sense. (1) After massive extinctions of hundreds of species during the first 1,000 iterations (sometimes lasting to 5,000) there was no change in diversity and relatively little change in abundance over 10,000–25,000 additional iterations. (2) After simulated removal of a fraction of the individuals of a persistent species, the abundances returned to preremoval values. (3) Simulated reintroduction of any species that had been driven to extinction invariably failed. This includes reintroduction of species with allocation strategies "between" those of the persistent species, indicating limiting similarity. Reintroductions were sometimes successful if the most similar persistent species was first removed. This is further evidence of limiting similarity.

We hypothesized that the species coexisted in the simulator by partitioning environmental heterogeneity created by the plants. Conditions (10), (11), (12), and (14) predict that a decrease in effective fecundity should increase limiting similarity (by increasing recruitment limitation) and should thus reduce species diversity. We tested this prediction by performing a series of runs that differed only in the value of g , the germination rate common to all species. In all cases, as predicted, the diversity and similarity of the persistent species decreased as g decreased. For example, in figure 7, we see the diversity collapse from seven to one species as g decreases from 0.1 to 0.001.

What is it that determines the relative competitive abilities of the species in

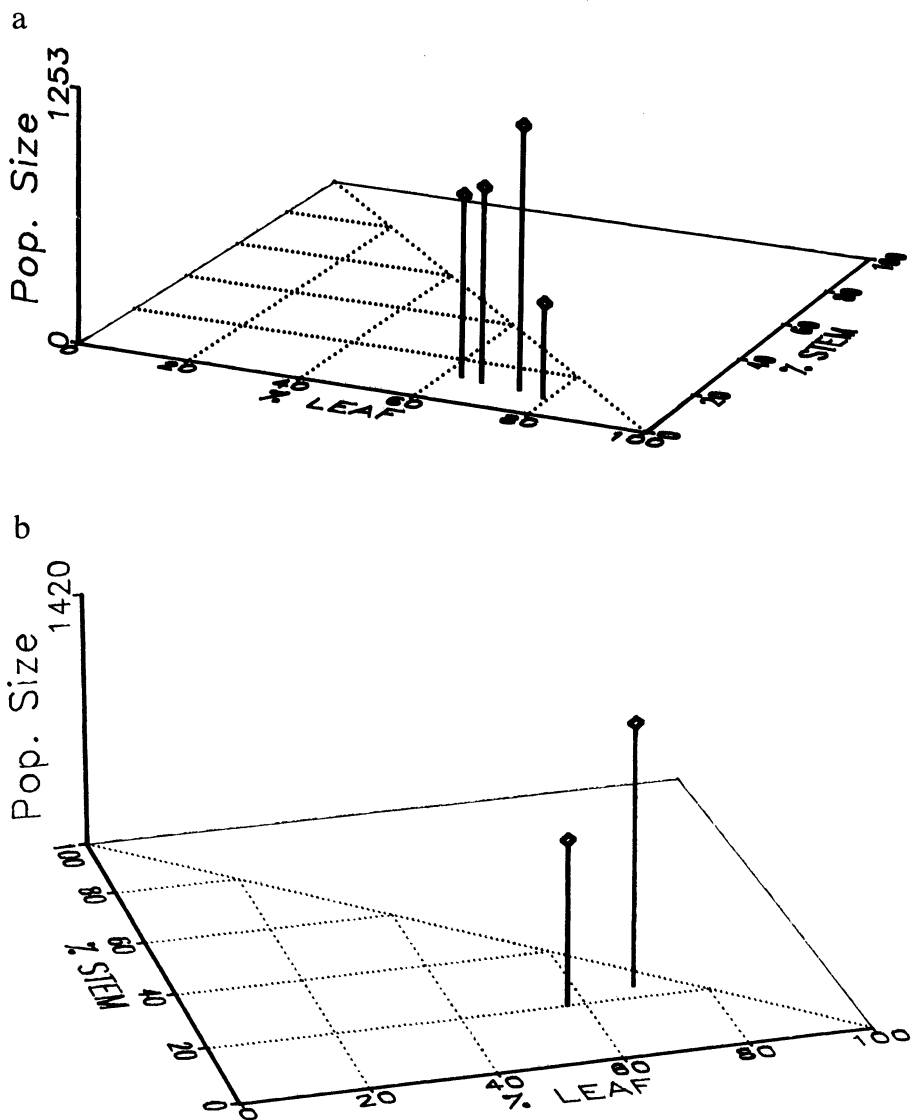
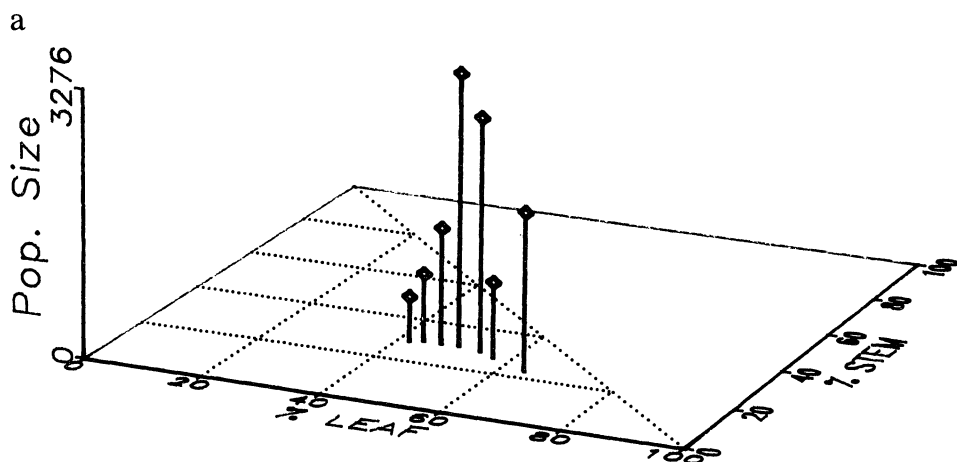
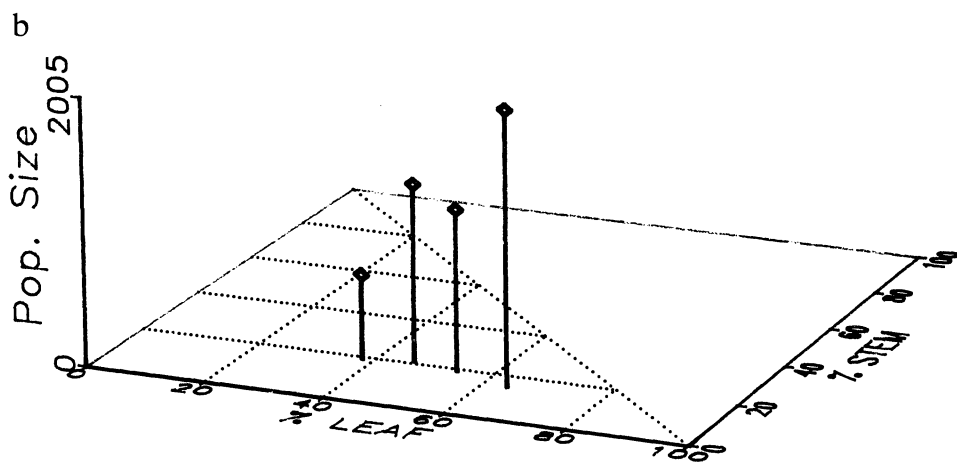


FIG. 6.—Examples of multispecies communities produced by the spatial simulation model. The *horizontal axes* show the allocation strategies of the species, and the *vertical axis* shows the population sizes at the approximate “equilibrium.” The parameter values for these runs are listed in App. B.

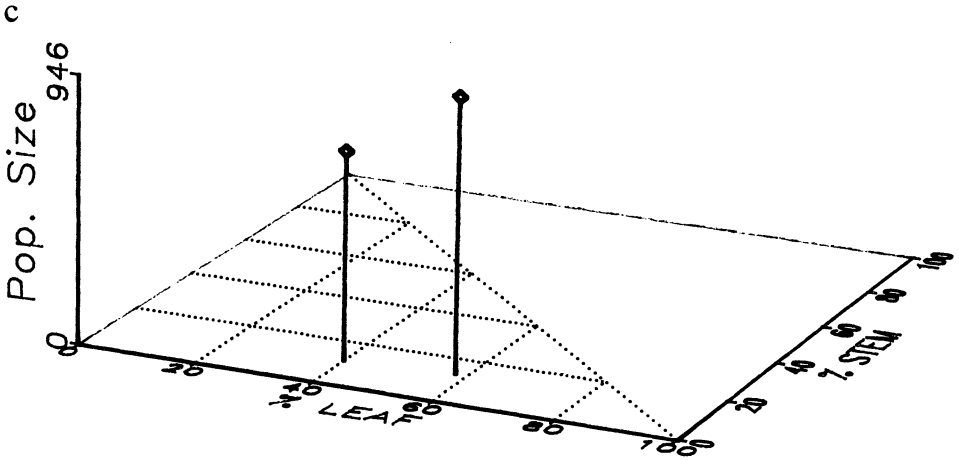


Germ. = 0.1

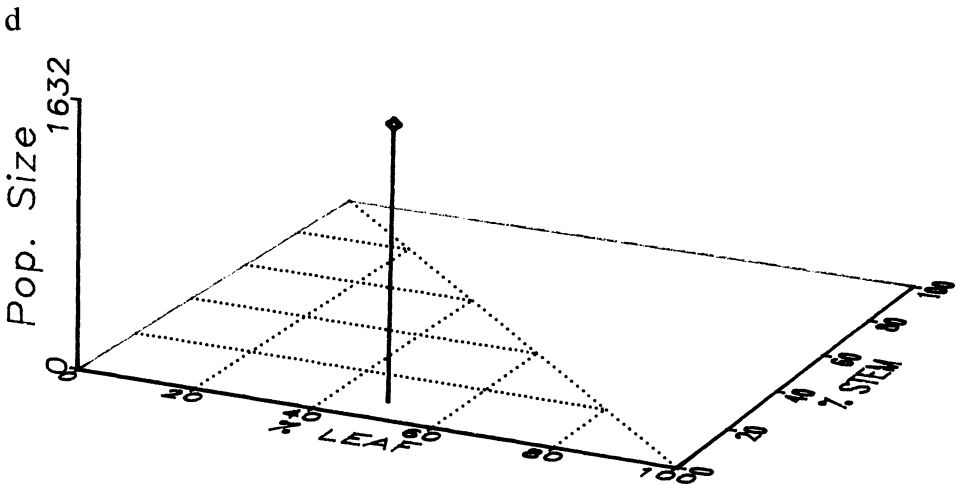


Germ. = 0.02

FIG. 7.—The effect of germination rate on equilibrium diversity and limiting similarity in the spatial simulation model. Note that diversity and similarity decrease as germination (and hence effective fecundity) decreases, as predicted by the analytically tractable models. The parameter values for these runs are given in App. B.



Germ. = 0.004



Germ. = 0.001

the simulator? This is a complex problem and we offer only a partial answer. Consider a suite of persistent species that share approximately the same percent allocation to stem (as in fig. 6). Because the growth rate of an individual is determined by available light and nutrient, an individual's success in reaching the canopy (the maximum height common to all species) is determined by the sequence of light and nutrient levels that it experiences. Species that differ in root and leaf allocation grew at different rates under the same conditions. We thus

hypothesized that time series of light and nutrient levels differed from place to place in the simulator, causing spatial variation, at any one time, in the most competitive allocation strategy.

We tested this hypothesis as follows. First, we observed that juveniles required 50–100 iterations of our model, on the average, to reach the canopy and that juveniles were quite small during most of this time (because of the exponential nature of growth). We then recorded a 100-yr time series of light and nutrient levels at ground level in each cell of simulations that had been run to equilibrium. Finally, we calculated the fraction, $\%leaf/(\%leaf + \%root)$, that yielded the fastest growth for each time series. We refer to this fraction as the optimal allocation strategy. Thus, for each persistent community, we had a histogram of from 100–300 optimal allocation strategies (one for each spatial cell) that we could compare to the allocation strategies of the species in the community. Invariably, the allocation strategies of the persistent species were centered on and contained by the histogram of optimal values (see the example in fig. 8).

Our most convincing demonstration that the persistent species coexist by partitioning spatial heterogeneity in time series of nutrient and light levels is shown in figure 9. These four runs differ only in the density-independent death rate shared by all species. Notice that, as the density-independent mortality rate increases, equilibrium species diversity first increases and then decreases (fig. 9a–d). This pattern is, of course, consistent with the pattern predicted by the intermediate disturbance hypothesis.

Histograms of optimal allocation strategies explain the pattern (fig. 9e–g). The arrows in figure 9e–g show the actual allocation strategies of the persistent species in runs 9a, c, and d. Diversity is low when the mortality rate is low (fig. 9a), because virtually all places share time series of light and nutrient levels that are characteristic of closed canopy. Because there is little spatial variation among these time series, there is little spatial variation among the optimal allocation strategies (fig. 9e). Thus, there exists an allocation strategy that is nearly optimal everywhere, and this strategy is clearly close to the strategy of the single persistent species in the run (the *arrow* in the figure).

In contrast, diversity is higher when the mortality rate is intermediate (fig. 9c) because intermediate rates lead to considerable spatial variance in time series of resource levels and corresponding optimal allocation strategies (fig. 9f). Note that the three persistent species in the run appear to partition this spatial variance (*arrows* in fig. 9f). With an intermediate mortality rate, some places, by chance, contain no canopy individuals that die over a 100-iteration period while others contain one or more such individuals. Multiple species coexist at equilibrium because each is the strongest competitor at the resource levels created by a different amount of local mortality. Figure 10 underscores this point. The figure shows, for the intermediate mortality rate in figure 9c and f, how the amount of random death within a cell during a 100-iteration period is related to the optimal allocation strategy for the period. Note that much of the variance in optimal allocation strategy is explained by random variation in local mortality. Apparently, each species in figure 9c persists by incessantly colonizing cells that subse-

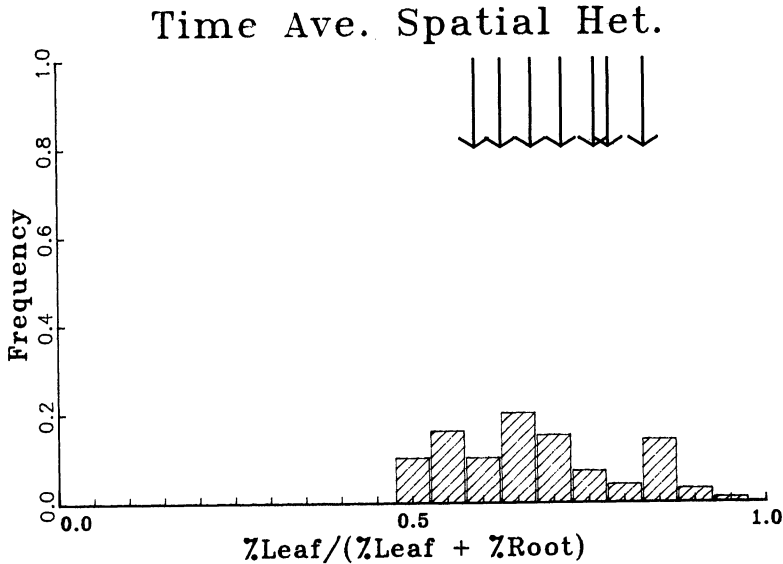
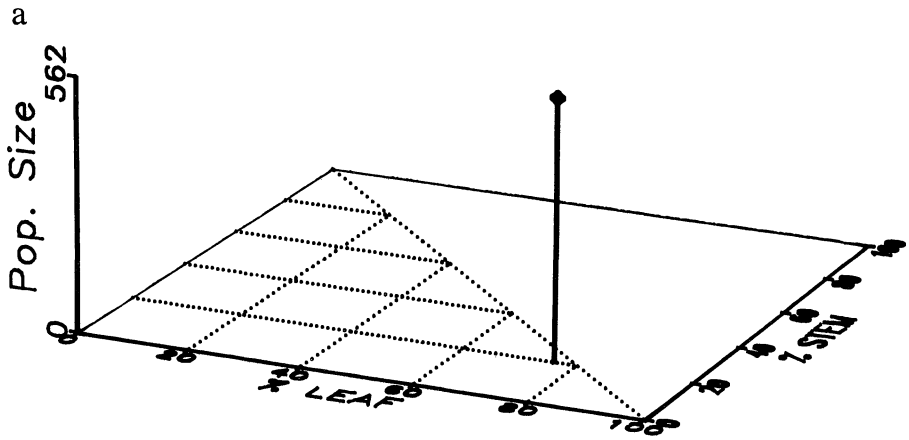


FIG. 8.—The spatial histogram of optimal allocation strategies ($\%leaf/[\%root + \%leaf]$) at equilibrium for the community shown in fig. 7a. To produce a histogram of optimal allocation strategies, we recorded 10-yr time series of light and nutrient levels, at ground level, in each cell of a model after it had been run to equilibrium. We then calculated the allocation strategy that yielded the fastest growth for each time series. The *arrows* show the actual allocation strategies of the seven species that coexist at equilibrium. Note that these are centered over the *spatial histogram* and appear to partition it.

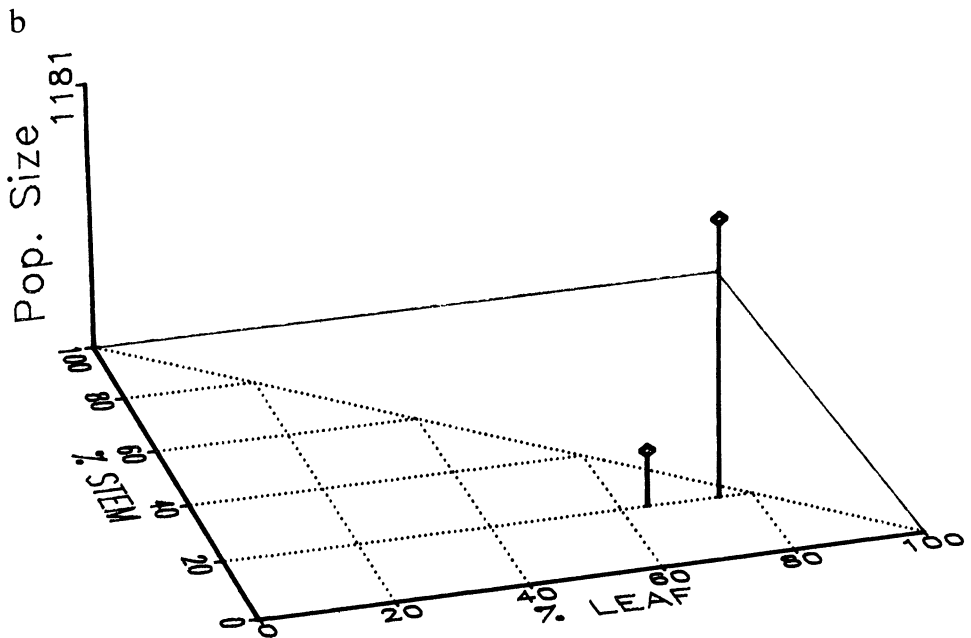
quently happen to have appropriate time series of resources because they happen to receive the appropriate level of local mortality.

Finally, high mortality rates lead to low species diversity (fig. 9d) because high levels effectively homogenize the habitat (fig. 9g). If the mortality rate is high enough, then the law of large numbers ensures that all cells will receive approximately the mean level of mortality. Thus, a single strategy is nearly optimal everywhere, and this strategy is again close to the strategy of the single persistent species. It is important to understand that the pattern in figure 9 is not an isolated example. To discover it, we selected four sets of parameters that produced steady-state multispecies communities and then systematically changed the density-independent mortality rate. We observed the pattern in figure 9 in all cases.

One of the most interesting things about figure 9 is that it illustrates the potential significance of demographic stochasticity (May 1974) in plant communities. May (1974) distinguished environmental stochasticity from demographic stochasticity. The former is caused by environmentally determined shifts in demographic parameters (say, because of changes in the weather), while the latter is caused by the inherent randomness of the demographic process itself (e.g., even with a constant mortality rate, the *number* of individuals that die in a finite population is a binomial random variable). Although demographic stochasticity is typically

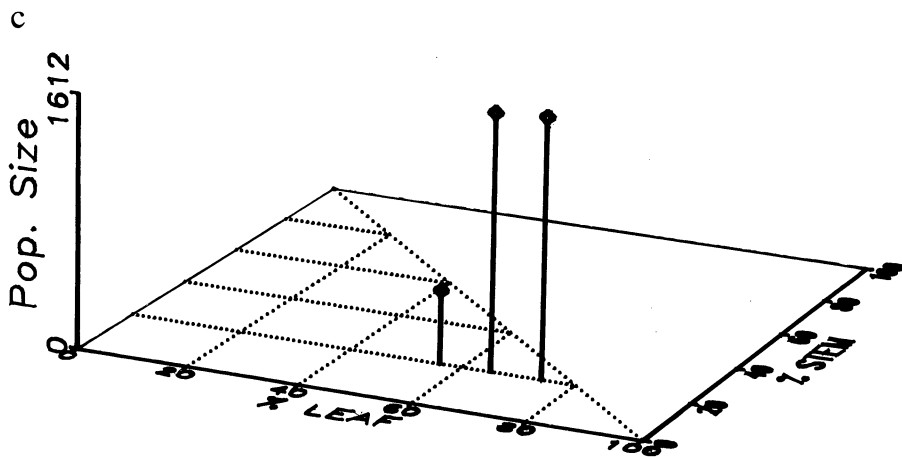


Death = 0.001

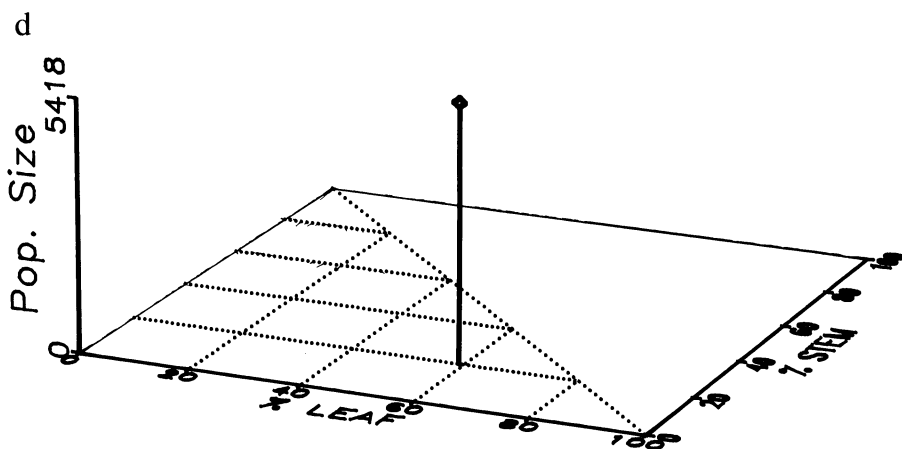


Death = 0.002

FIG. 9.—The intermediate disturbance hypothesis (parts *c–g* are on following pages). The runs producing *a–d* differ only in the density-independent death rate shared by all species. As disturbance increases, diversity first increases (*a–c*) and then decreases (*c–d*). *e*, The spatial histogram of optimal allocation strategies for the species in *a*. *f* and *g*, Similar histograms for the species in *c* and *d*, respectively. To produce a histogram of optimal allocation strategies, we recorded 10-yr time series of light and nutrient levels, at ground level, in each cell of a model after it had been run to equilibrium. We then calculated the allocation strategy that yielded the fastest growth for each time series. The arrows in *e*, *f*, and *g* show the allocation strategies of the species in *a*, *c*, and *d*, respectively. Note that species coexist in *c* by partitioning the relatively large variance of the histogram in *f*. Parameter values for all runs are listed in App. B.



Death = 0.01



Death = 0.1

FIG. 9.—(Continued)

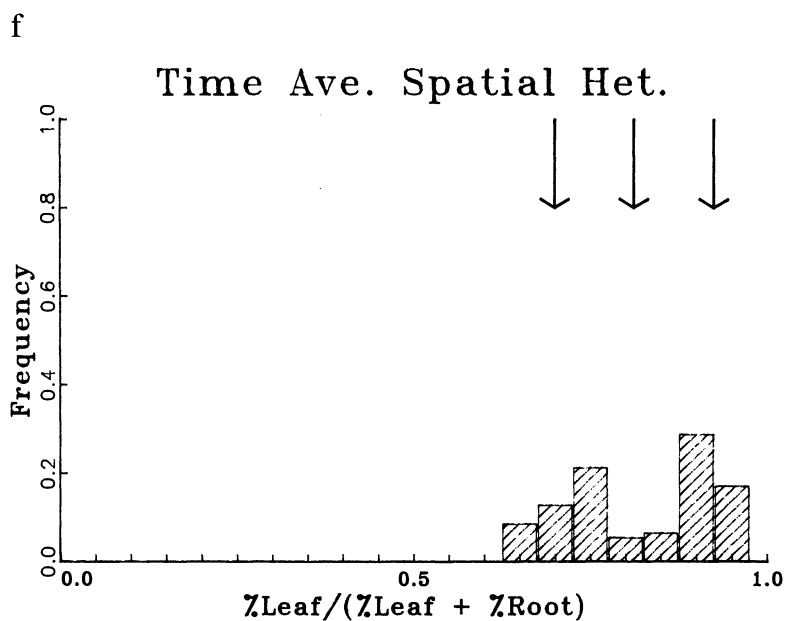
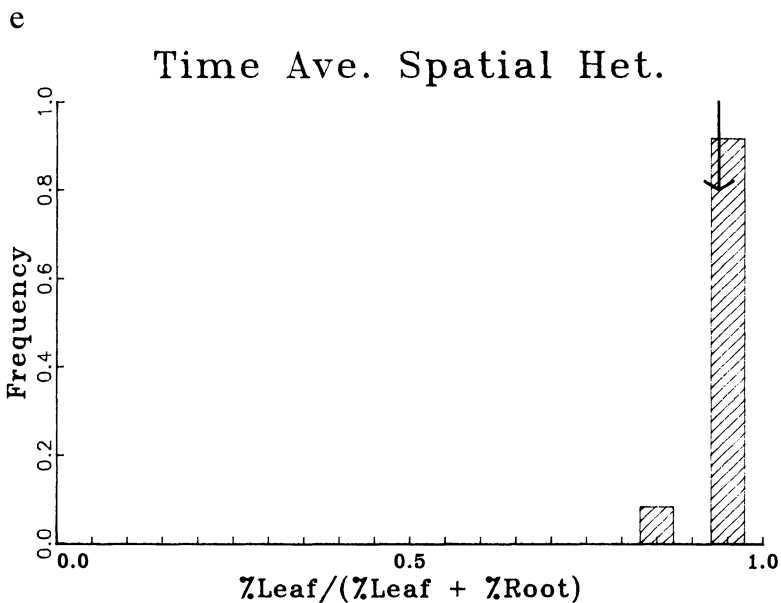


FIG. 9.—(Continued)

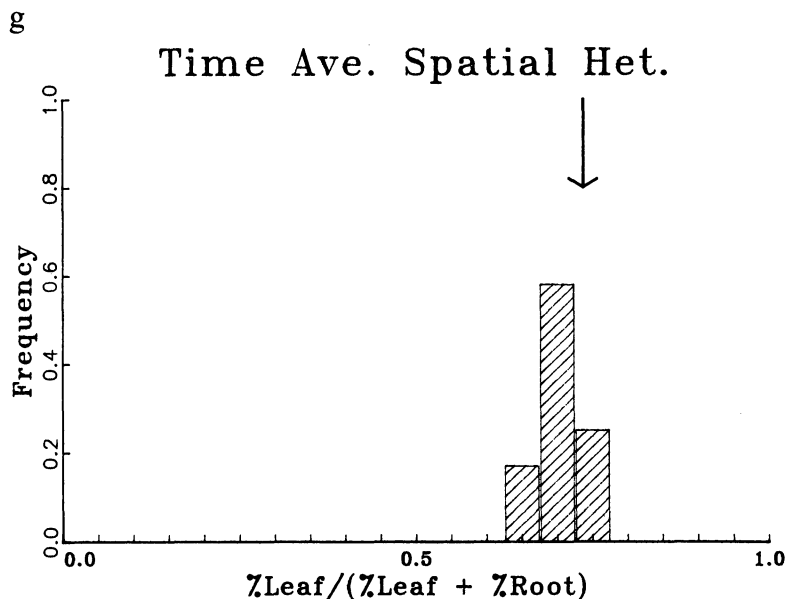


FIG. 9.—(Continued)

viewed as a weak force in large populations, the examples shown here demonstrate that it can create partitionable variance that maintains diversity. Most of the dead biomass in figure 10 consisted of dead canopy adults. Because there were relatively few canopy individuals in each of the model's cells and because these had a relatively large effect on local resource availability, demographic stochasticity was able to create the large between-cell variance in resource levels that leads to coexistence.

DISCUSSION

In this article, we offer a series of examples in which mechanistic submodels determine the outcome of competition among juveniles that vie for possession of spatial cells left vacant when adults die. A superspecies does not exist because of assumed trade-offs (the universes of possible species) that limit the range of environmental conditions in which each species is competitively superior. In unpredictable environments, each species is a fugitive that persists if it can successfully disperse from the place to place and/or the time to time in which it is the strongest competitor. Note that "fugitive species" is used here in a nonstandard context. Instead of species that temporarily occupy recently disturbed locations before dominant competitors arrive, all species that persist in our model are competitively dominant under some environmental conditions.

Our principal result is that limiting similarities exist in simple mechanistic models of plant competition. If species are too similar, then at least one species is driven to extinction because the range of environmental conditions in which it is the strongest competitor is too narrow. Its progeny are then too rare, on the

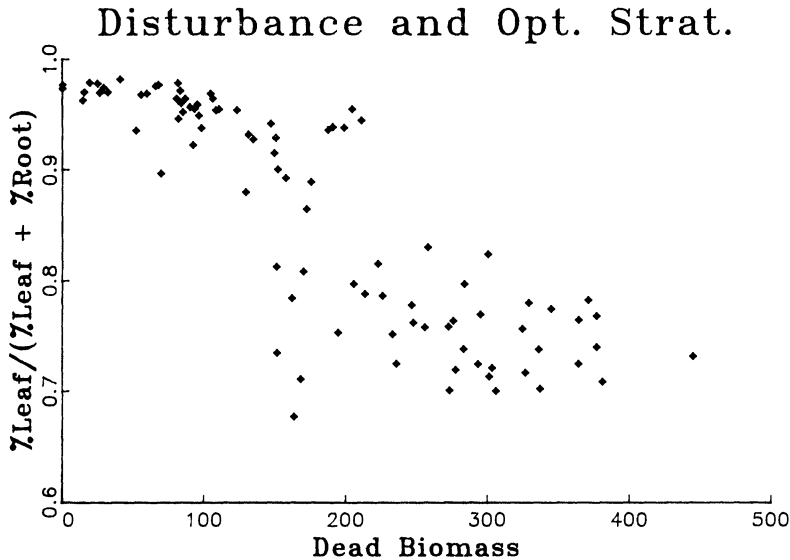


FIG. 10.—The relationship between local mortality and optimal allocation strategy for the run illustrated in fig. 9c and f. Each *point* shows the optimal allocation strategy for a spatial cell during a 100-iteration time period and the amount of biomass that died in that cell during the period. The variance along the *horizontal axis* is due entirely to demographic stochasticity. Note that demographic stochasticity apparently causes the variance among optimal allocation strategies in fig. 9f that, in turn, apparently maintains the diversity shown in fig. 9c.

average, to locate the rare times and places in which environmental conditions allow it to compete successfully.

We do not know whether limiting similarities structure plant communities in nature. On the one hand, coexisting forest tree species in many locations appear to partition spatial and temporal variation in light levels (Horn 1971). For example, dominant species in the northern hardwood community in northeastern North America appear to coexist by partitioning demographic stochasticity, much as in the computer simulation model discussed above (Canham 1988). Similarly, there are many examples of species that appear to coexist by partitioning environmental heterogeneity that affects seedling performance during regeneration (see examples in Grubb 1977, 1986; Chesson and Huntly 1988, 1989). On the other hand, the experience of animal ecologists with MacArthur's resource-partitioning models during the 1970s illustrates the dangers of inferring too much from correspondence between predicted and observed patterns of community structure. Many processes can lead to the same patterns. Moreover, the enormous tree diversity in tropical forests is difficult to reconcile with a conclusion that limiting similarity constrains the diversity of tropical plant communities (Hubbell and Foster 1986).

The prediction of limiting similarity itself hinges on two propositions. First, the prediction requires the somewhat-controversial assumption that interspecific

trade-offs in competitive ability exist—that the relative competitive abilities of plant species change in response to changes in environmental conditions. Nonetheless, this proposition is supported by numerous experimental studies of natural communities (see the many examples in Harper 1977) and is a principal motivation for work on multicropping agricultural systems (Francis 1986). Second, plant species must be recruitment limited—species must sometimes fail to colonize pockets of space and time in which environmental conditions make them strong competitors. Although intertidal ecologists have demonstrated that recruitment limitation is important in some intertidal communities (Roughgarden et al. 1988), the subject has received little attention by terrestrial plant ecologists (but see Shmida and Ellner 1984; Alvarez-Buylla and Garcia-Barros 1991). Forest simulators such as FORET (Shugart 1984) and Markov forest models (Horn 1975, 1976) assume that there is no coupling between the number of juveniles in a site and the resident community of adults. These models thus assume that recruitment limitation is either unimportant or that rare and common species are equally affected. Even so, our theoretical results, the findings of intertidal ecologists, and the empirical evidence that does exist for terrestrial plants suggest that the recruitment limitation is likely to be an important determinant of plant community structure.

Although our approach has been to develop results using simple models that permit analytical solution, we have attempted to assess the generality of these results in three ways. First, we have included three distinct mechanistic submodels of competition to illustrate that our results apply to a wide range of processes and universes of possible species. With these as guides it is straightforward to formulate other models in which mutualists, natural enemies, resources, and physical factors, alone or in concert, affect the outcome of competition among plants and lead to limiting similarity. Perhaps the most restrictive simplifying assumption shared by these submodels is that each predicts the competitive exclusion of all save one plant species in a homogeneous environment. Clearly, submodels that predict deterministic coexistence among a subset of the species in a homogeneous habitat should be incorporated into future models. We suspect that these would predict higher diversity than the models discussed here and reduced importance of limiting similarity. On the other hand, such models might expose limiting similarities with other causes (e.g., resource partitioning in the classical niche-theoretic models). Even so, the large number of published experiments indicating competitive exclusion (reviewed in Harper 1977) argues that the approach taken here is perhaps not overly unrealistic.

Second, we have shown that our results are robust to changes in the nature and origin of environmental heterogeneity. For example, limiting similarities are predicted if heterogeneity is entirely spatial, entirely temporal, or a mixture of the two. It is predicted if the heterogeneity is physical (e.g., variations in temperature) or biotic. The biotic heterogeneity may be caused by the plants themselves (e.g., local variation in adult biomass due to random deaths of adults) or by other organisms (e.g., herbivores). Finally, limiting similarities are predicted, in some cases, if local environments are spatially and temporally autocorrelated because

of biotic factors (e.g., species-specific differences in the litter chemistry of adults that affect future resource availability) or because of physical factors (e.g., heterogeneous geologic parent material of soils).

Even so, our modeling of heterogeneity is probably unrealistically simple in a number of ways. In particular, we assume in all of the analytically tractable models that the spatial scale of environmental variation is never smaller than the size of a single cell. This assumption greatly simplifies the mathematics because it allows us to ignore the number of juveniles of each species in each cell and focus exclusively on presence or absence. If the most competitive species is present in a cell, then it captures it regardless of the numbers of juveniles of other species. Of course, in nature, there is heterogeneity among the performances of conspecific juveniles in the same location caused by such factors as fine-scale heterogeneity of soils, stochastic variation in levels of herbivory or pathogen infection, age structure, and genetic polymorphism. If we were to include interindividual differences among the performances of conspecifics, then we would have to compare the performances of all individuals to determine the competitive dominant rather than simply rank the competitive abilities of species. Because interindividual heterogeneity would reduce the number of contenders that have the potential to dominate a cell we suspect that it would reduce the effective fecundity of each species (F) and thus *increase* the limiting similarity (see conditions [10], [13], and [15]). For example, suppose that each juvenile has a probability, H_i , of escaping an infection that limits performance. Because cells will be captured primarily by uninfected juveniles, the average effective fecundity is approximately $H_i F$, which is less than F . Thus, fine-scale heterogeneity has the potential to increase the magnitude and importance of limiting similarity.

The final evidence that our results are robust to changes in the assumptions of the simple analytically tractable models is offered by the simulation model. This model contains few of the assumptions of the simple models and yet produces qualitatively similar results. For example, the simulator contains finite numbers of individuals, age-structured interjuvenile heterogeneity, two axes in the universe of possible species, and asymmetric competition for light. It allows multiple adults and juveniles to occupy the same cell, contains no explicit assumptions prohibiting coexistence under homogeneous conditions, and operates in continuous time so that succession is not, as in the simple models, instantaneous. Time is required to become locally dominant in the simulator just as it is in natural systems. Finally, the simulator allows all species to be simultaneously recruitment limited, rather than only a single rare invading species. We were frankly surprised that the simulator produced familiar niche-theoretic results and now suspect that MacArthur's ideas may lurk in the code of other forest simulators.

Environmental heterogeneity has many causes that may vary among plant communities, but some sources of environmental heterogeneity are inevitable. For example, species in the simulation model apparently coexist by partitioning heterogeneity in resource levels caused by spatially local demographic stochasticity (local stochastic variation in the amount of canopy mortality). It is possible that the widespread occurrence of communities of coexisting tree species that differ

in shade tolerance is a reflection of the inevitability of demographic stochasticity. We suggest that the search for inevitable sources of heterogeneity may lead to the discovery and understanding of structure shared by many plant communities.

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APPENDIX A

THE DERIVATION OF CONDITIONS (10) AND (11)

In this appendix, we derive conditions (10) and (11) for the instability of a boundary equilibrium in a system of W patches. We ask: When can a locally stable equilibrium community of Q resident species (species 1, 2, 3, . . . , Q) be invaded by a rare invader (species I)? Dynamics are governed by W different equations for each species. The equations for the invading species are

$$\begin{aligned}\Delta X_{Ik} &= -d_{Ik}X_{Ik} + d_{Ik}X_{Ik}p_{II}^k(1 - H_{Ik}) + \sum_{j=1}^Q d_{jk}X_{jk}p_{Ij}^k(1 - Z_{Ik}) + \sum_{j=1}^Q O_j(Z_{jk}), \\ H_{Ik} &= [(1 - m_{IS} - m_{IL})(1 - g_{Ik}) + m_{IS} + m_{IL}]^{F_{Ik}}Z_{Ik}, \\ Z_{Ik} &= \exp(-g_{Ik} \sum_{v=1}^W [F_{Iv}X_{Iv}m_{IL}] - g_{Ik}X_{Ik}F_{Ik}M_{IS}),\end{aligned}\tag{A1}$$

and

$$k = 1, 2, \dots, W,$$

where H_{Ik} gives the probability that no species I juveniles are present in a cell just vacated by a species I adult, Z_{Ik} gives the corresponding probability for a cell just vacated by any of the resident species, and $O_j(Z_{jk})$ is a term of order Z_{jk} .

Because the quantity $\partial\Delta X_{Ik}/\partial X_{Iv}$ ($j = 1, 2, \dots, Q$; $k = 1, 2, \dots, W$; $v = 1, 2, \dots, W$) is invariably zero when evaluated at the boundary equilibrium, the $W(Q + 1) \times W(Q + 1)$ Jacobian matrix governing the stability of the boundary decomposes into two blocks. One $WQ \times WQ$ block governs the stability of the resident community in the absence of the invader. This block yields eigenvalues within the unit circle (centered at $(-1, 0)$) on the complex plane because of the assumption that the resident community is locally stable in the absence of the invader. The remaining $Q \times Q$ block determines the success of invasion and is referred to below as the stability matrix J . The characteristic equation for the eigenvalues governing the stability of the boundary is thus

$$|J| = 0 = \begin{vmatrix} A_1 + B_1C_1 & B_1C_2 & \cdot & \cdot & B_1C_Q \\ B_2C_1 & A_2 + B_2C_2 & \cdot & \cdot & B_2C_Q \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ B_QC_1 & B_QC_2 & \cdot & \cdot & A_Q + B_QC_Q \end{vmatrix},\tag{A2}$$

where $A_k = -d_{Ik} + d_{Ik}p_{II}^k(1 - H_{Ik}) + g_{Ik}F_{Ik}M_{IS} \sum_{j=1}^Q d_{Jk}X_{jk}^*p_{Ij}^k - \lambda$, $B_k = g_{Ik} \sum_{j=1}^Q d_{jk}X_{jk}^*p_{Ij}^k$, $C_k = F_{Ik}m_{IL}$, and λ signifies an eigenvalue. In writing equation (A2), we have ignored all terms of order Z_{jk}^* (the asterisk signifies evaluation at the boundary equilibrium) because of our assumption that the residents are not recruitment limited.

We now indulge in two algebraic tricks. We first subtract B_k/B_Q times the last row in J from each k th row ($k = 1, 2, \dots, Q - 1$). We then reverse the order of the subscripts so that the subscript Q becomes 1, 1 becomes Q , $Q - 1$ becomes 2, and so on. The result is the characteristic equation

$$0 = \begin{vmatrix} A_Q & 0 & \cdots & 0 & 0 & -\frac{A_1 B_Q}{B_1} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & \cdots & A_3 & 0 & -\frac{A_1 B_3}{B_1} \\ 0 & 0 & \cdots & 0 & A_2 & -\frac{A_1 B_2}{B_1} \\ B_1 C_Q & B_1 C_{Q-1} & \cdots & B_1 C_3 & B_1 C_2 & A_1 + B_1 C_1 \end{vmatrix} \quad (\text{A3})$$

Now, let D_i be the determinant of the $i \times i$ submatrix in the lower left-hand corner of equation (A3). Thus, $D_1 = A_1 + B_1 C_1$, $D_2 = A_2 D_1 + A_1 B_2 C_2$, $D_3 = A_3 D_2 + A_1 A_2 B_3 C_3$, and $D_Q = A_Q D_{Q-1} + [\prod_{j=1}^{Q-1} A_j] B_Q C_Q$. After expanding the above expression, we may use it to write equation (A3) as

$$0 = A_1 A_2 \cdots A_Q + B_1 C_1 A_2 A_3 \cdots A_Q + A_1 B_2 C_2 A_3 \cdots A_Q + \cdots + A_1 A_2 \cdots A_{Q-1} B_Q C_Q. \quad (\text{A4})$$

We now divide both sides of equation (A4) by $A_1 A_2 \cdots A_Q$ and rearrange:

$$1 = \sum_{i=1}^Q \frac{b_i}{a_i + \lambda}, \quad (\text{A5})$$

where $a_i = -A_i - \lambda$ and $b_i = B_i C_i$ (a_i and b_i are the same as in conditions [10]–[11] in the text). Note that $b_i \geq 0$ and that a_i and b_i are independent of λ .

We now show that all eigenvalues given by equations (A4) and (A5) are real. First, by inspection of equation (A4), for each $b_i = 0$, there exists a corresponding real eigenvalue equal to $-a_i$. Second, note that the right-hand side of equation (A5) approaches zero from below as λ approaches $-\infty$, approaches zero from above as λ approaches $+\infty$, and has a pole at $\lambda = -a_i$ (because of zero in a denominator) for each term in which $b_i > 0$. A simple graph of these properties is sufficient to show that there is a single real root for each term in which $b_i > 0$.

Because the eigenvalues are real, invasion succeeds if and only if there is at least one positive eigenvalue. There are four separate cases. First, suppose that $a_i < 0$ and $b_i = 0$ for some i . Then, as stated above, $-a_i$ is an eigenvalue and invasion succeeds. Second, suppose that $a_i \leq 0$ and $b_i > 0$ for some i . The right-hand side of equation (A5) approaches $+\infty$ as λ decreases toward $-a_i$ and decreases to zero as λ approaches $+\infty$. Thus, the right-hand side of equation (A5) must cross one at a (positive) value of λ between $-a_i$ and ∞ and so invasion succeeds. Third, suppose that $a_i > 0$ for all i . Then, the right-hand side of equation (A5) decreases monotonically from a positive value to zero as λ increases from zero to ∞ . Invasion succeeds (because there is a single positive eigenvalue) if and only if the right-hand side of equation (A5) evaluated at $\lambda = 0$ is greater than one. In the one remaining case, $a_i \geq 0$ for all i and $a_i = b_i = 0$ for at least one i . By inspection of

equation (A4), there is at least one eigenvalue equal to zero. Now suppose that we eliminate the term(s) for which $a_i = b_i = 0$ from the summation in equation (A5). As in the third case (above), there will be a positive eigenvalue and invasion will succeed if the resulting sum is greater than one when evaluated at $\lambda = 0$. Otherwise, the local analysis is inconclusive (neutral stability to first order). Observe that condition (11) in the text handles the first two cases above while condition (12) handles the last two.

APPENDIX B

THE DESIGN OF THE SPATIAL SIMULATION MODEL

In this appendix, we describe the spatial version of the simulator developed in Tilman (1988). The habitat is composed of CELLS spatial cells and a run is initiated by placing INUM seedlings of each species randomly across the habitat. The biomass of a seedling is ISIZE. Species differ only in allocation pattern. The biomass of an individual of species i is a fraction $R[i]$ roots, $L[i]$ leaves, and the rest stem. A run is initiated with all possible species that differ by at least $AINT$ in allocation pattern. For example, if $AINT = 0.05$, then the run contains species with 5% root, 10% root, and so on. To ensure that species have time to establish, a single additional seedling of each species is added to the habitat in each of the first SDRAIN iterations.

The duration of an iteration is DT . In each iteration, we first determine light and nutrient levels. The light level experienced by a plant is e^{-ALUB} , where AL is the light extinction constant and UB is the total biomass of leaves of all taller plants in the same cell. Nutrient availability is determined as follows. In each cell, there is $MAXNUT$ total nutrient. In cell j , $TNB[j]$ is incorporated into plant biomass, $NUT[j]$ is available for use by plants, and the remainder ($UN[j]$) is unavailable. When biomass dies, the nutrient in it enters the unavailable pool. An amount, $DT \times AN \times UN[j]$, becomes available in each iteration where AN is a constant. Plants are a fraction PN nutrient and so $TNB[j]$ equals the total biomass in cell j times PN .

After nutrient and light levels are determined, each plant grows by an amount

$$DT \left(\min \left[\frac{r RB[i] NUT[j]}{KN + \frac{RB[i] NUT[j]}{LB[i]}}, \frac{r LB[i] LITE[i]}{KL + LITE[i]} \right] - RESP BIOM[i] \right), \quad (B1)$$

where $RB[i]$, $LB[i]$, $BIOM[i]$, and $LITE[i]$ are, respectively, the root biomass, leaf biomass, total biomass, and light level for the i th individual. Also, r is the maximum production rate, KN and KL are half-saturation constants, and $RESP$ is the respiration rate.

The maximum stem biomass of a plant is MHT and height is assumed to be proportional to stem biomass. Plants approach the maximum height logistically. A fraction, $1 - STEM-BIOMASS[i]/MHT$, of the growth given by equation (B1) is added to the i th plant's biomass, and the remainder is converted into seeds. The number of seeds produced is equal to the biomass devoted to seed production divided by $ISIZE$. Seeds are distributed randomly over the plot and germinate with probability $GERM$. After growth and reproduction, plants die if they have negative growth or randomly with probability $MORT$.

Parameter values in the figures.—In each of figures 6–10, $CELLS = 100$, $INUM = 25$, $ISIZE = 0.1$, $DT = 1$, $KL = 0.2$, $MHT = 10$, $AN = 1.0$, and $SDRAIN = 100$. In figures 6a, 7, and 8, $AINT = 0.02$; elsewhere, $AINT = 0.01$. In all figures except 6a, $PN = 0.01$ and $RESP = 0.04$; in figure 6a, $PN = 0.1$ and $RESP = 0.4$. The remaining values are as follows: $AL = 0.02$ (fig. 6a), 0.05 (figs. 7–8), and 0.1 in all others; $r = 2.0$ (fig. 6a), 4.0 (figs. 7–8), and 1.0 in all others; $GERM = 0.1$ (figs. 6a, 7a, and 8), 0.05 (fig. 6b), 0.02

(fig. 7b), 0.004 (fig. 7c), 0.001 (fig. 7d), and 0.25 (figs. 9–10); MAXNUT = 50 (fig. 6a), 5 (figs. 6b, 9–10), and 500 (figs. 7–8); KN = 10 (fig. 6a), 0.2 (figs. 6b, 9–10), and 2,000 (figs. 7–8); and MORT = 0.01 (figs. 6–8, 9c, f, 10), 0.001 (figs. 9a, e), 0.002 (fig. 9b) and 0.1 (fig. 9d, g). Finally, the runs in figures 9–10 are unlike the others in that all species present were constrained to have the same stem allocation of 0.2.

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