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COMPLEX INTERACTIONS IN METACOMMUNITIES, WITH IMPLICATIONS FOR BIODIVERSITY AND HIGHER LEVELS OF SELECTION¹

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Abstract. Two common features of biological communities are (a) complex interactions among species, which make community dynamics sensitive to initial conditions, and (b) spatial heterogeneity, which fragments large-scale ecological systems into a mosaic of patches, hereafter termed a “metacommunity.” This computer simulation study examines the effect of complex interactions on the global and local dynamics of metacommunities. Patches are physically identical and differ only in the initial proportion of species that colonize the patches. The random variation is then magnified by deterministic interactions that cause patches to follow different trajectories based on initial conditions. After a period of interaction, individuals from all patches join a global pool of dispersers that colonize a new “generation” of patches.

Complex interactions can have at least two important effects on metacommunity dynamics. First, the number of species coexisting in the metacommunity can greatly exceed the number of species coexisting in any single patch, despite the fact that the patches are physically identical, the species do not differ in colonization ability, and stochastic effects are absent after the colonization stage. Second, complex interactions provide a new source of variation upon which natural selection can operate at the patch level, providing a mechanism for the evolution of functionally organized communities.

Key words: biodiversity; chaos; community selection; complex interactions; group selection; metacommunity; metapopulation; population structure; sensitive dependence; spatial heterogeneity; species diversity; superorganisms.

INTRODUCTION

A great deal of attention has been focused recently on complex interactions among species, leading to dynamics that are difficult to predict or even truly chaotic (Segel and Jackson 1972, Guckenheimer et al. 1977, Robinson and Edgemon 1988, Yodzis 1988, Berryman and Millstein 1989, May 1989, Ornstein 1989, Drake 1990a, b, Strauss 1991). One common feature of complex interactions, chaotic and otherwise, is *sensitive dependence on initial conditions*, in which small perturbations have large effects on the outcome of deterministic interactions.

Although the importance of true chaos in nature is debatable (Berryman and Millstein 1989, Pool 1989, Olsen and Schaffer 1990), there is little doubt that the dynamics of biological communities are often sensitive to initial conditions. For example, Drake (1991, 1992) and Robinson and Edgemon (1988) have shown that aquatic microcosm communities are influenced by the *sequence* in which the species are introduced. More generally, many community ecologists have had the unpleasant experience of setting up replicated experiments and watching differences develop among replicates that rival the magnitude of differences between treatments (examples in Hurlbert 1984). Although un-

looked for and unwelcome, these within-treatment effects provide inadvertent evidence that small initial differences among replicates can be magnified by subsequent interactions.

This computer simulation study examines complex interactions in communities that are broken up into a mosaic of patches, hereafter termed a “metacommunity.” The basic idea behind the simulations can be described as follows: In an S -species metacommunity, let p_{ij} be the proportion of species i in patch j . A single patch can be represented by a point in S -dimensional space ($p_{1,j}, p_{2,j}, \dots, p_{S,j}$), and the entire metacommunity can be represented by a cloud of points whose size and shape reflect variation in patch species composition. Let all patches be colonized at random by N individuals from a pool of dispersers, creating a “cloud of variation” that is determined purely by sampling error. Now allow the species to interact deterministically within each patch for a period of time. If species interactions lead to a single global equilibrium, then the cloud of variation will shrink to a single point as the patches converge on the equilibrium. With more complex interactions, however, the patches might follow different trajectories through S -space, depending on their initial composition—much like the replicates of a community ecology experiment. Deterministic interactions would then have the effect of expanding the initially random cloud of variation.

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Viewing metacommunities as a dynamical cloud of variation has at least two important implications for community ecology. First, complex interactions can provide a source of endogenous variation that promotes biodiversity, even when patches are physically identical and environmental stochasticity is absent. Second, complex interactions provide a new source of variation upon which natural selection can operate at the patch level, facilitating the evolution of functionally organized communities.

A MODEL

Translating the preceding verbal sketch into a simulation model requires a large number of specific assumptions that restricts analysis to a tiny fraction of the parameter space. The following model should therefore be regarded as a first effort to explore a very complicated process.

Metacommunity structure

Consider a metacommunity consisting of a large number of discrete patches. The patches can be connected by dispersal in at least three ways (reviewed by Hartl and Clark 1989, Hanski and Gilpin 1991). First, a fraction of individuals from a given patch might travel to adjacent patches (often referred to as the "stepping-stone model," e.g., Hassel et al. 1991). Second, a fraction of individuals might join a global pool of dispersers that travel to all patches with equal probability (often referred to as the "island model," e.g., Gotelli 1991). These models assume that patches are like an archipelago of islands that persist indefinitely, although the populations and communities that occupy them may wink in and out of existence. A third model (often called the "subdivided-population model") assumes that the patches are by nature ephemeral, such as a host organism occupied by a community of endosymbionts or a dead tree occupied by a saprophytic community. In this case all patches have a fixed maximum lifetime and their occupants must join a dispersal pool to colonize a new set of empty patches. Obviously, most natural metacommunities are mixtures of the extremes represented by these three models.

The following simulations are based on the subdivided-population model and can be described as a number of stages: (1) A global pool of dispersers exists with 10 species in relative proportions p_1, p_2, \dots, p_{10} . (2) A large number (T) of discrete patches are each colonized at random by N individuals from the global pool. By this process each patch receives a subset of the 10 species in proportions that deviate by chance from the global proportions. (3) For one set of simulations, patches become "closed" to colonization after stage 2. For another set of simulations, patches remain open to colonization, but the initial density of latecomers is assumed to be low relative to the density of the N firstcomers, who have had the opportunity to reproduce within the patches. This is modelled by

maintaining all species in all patches at a minimal background density of $B = 0.1$. (4) Deterministic interactions occur within each patch by iterating a set of difference equations (described in detail below; see *Interactions within patches*) a number (J) of times. For the open colonization runs, species that go extinct are reset to the background density of $B = 0.1$. (5) All individuals disperse back into the global pool, and new global proportions (p_1, p_2, \dots, p_{10}) are calculated. (6) Stages 1–5 are repeated for a number (C) of cycles that can be regarded as patch-level "generations."

Most of the specific assumptions listed above are intended to be conservative. Subdivided-population models are more like a single unstructured population than are island and stepping-stone models because the spatial heterogeneity that is established during stages 2–4 is completely erased during stage 5. The synchronized nature of patch colonization and dispersal, like the discrete generations of population genetics models, is not an essential feature. Assuming a large enough metacommunity, similar results would pertain if patches winked on and off out of phase with each other. The B term reflects a number of biological considerations. In natural metacommunities, species that fail to initially colonize a patch may well arrive later, after other species have become established. The background density assures that no species is permanently excluded from a patch and also that no species goes extinct, locally or globally. This is often biologically reasonable because colonists can enter a metacommunity from other areas, despite the fact that they do not thrive within the metacommunity.

To monitor the effect of complex interactions on the "cloud of variation," the variance in the proportion of each species among patches was calculated immediately after colonization and after J iterations of the difference equations (i.e., immediately before dispersal). The actual shapes of the distributions and the covariance of species proportions was also examined for selected cases.

It is important to emphasize that this model does not include features common to other models of communities in structured populations. In particular, species do not differ in their colonizing ability (sensu Levin and Paine 1974, Levin 1976), and stochastic effects (sensu Chesson 1983, Chesson and Huntly 1988) are absent apart from determining initial patch composition.

Interactions within patches

The dynamics of species interactions can be modelled in literally dozens of ways. I begin at the simplest level with the Lotka-Volterra competition equations (MacArthur 1972).

$$N_{i,t+1} = N_{i,t} \left[1 + \frac{R}{K} \left(K - \sum_{j=1}^S N_{j,t} \alpha_{ij} \right) \right] \quad (1)$$

$N_{i,t+1}$ refers to the density of species i during the next

time interval. K is the carrying capacity, R governs the rate of increase, and α_{ij} is the per capita effect of species j on species i . I make the following additional assumptions: (1) Eq. 1 applies to all patches in the metacommunity, which implies that the patches are identical in their physical characteristics and differ only in their species composition; (2) All species have the same rate of increase (R) and carrying capacity (K); (3) All direct interactions are competitive ($\alpha_{ij} > 0$); (4) Per capita effects of species on themselves are unity ($\alpha_{ii} = 1$); (5) Per capita effects of species on other species (α_{ij} , $i \neq j$) are random numbers uniformly distributed between 0 and 2. Thus, other species on average have the same negative effect as conspecifics, but particular other species can have either a greater ($\alpha_{ij} > 1$) or a lesser ($\alpha_{ij} < 1$) effect.

Despite the simplicity of these equations, they provide ample potential for complex interactions, including multiple stable equilibria (Gilpin and Case 1976, Pomerantz and Gilpin 1979, Drake 1990b) and so-called "indirect effects," whereby species influence each other not only through their interaction coefficients (α_{ij}) but through their effects on the density of other species in the patch (Levins 1975, reviewed by Strauss 1991). Indirect effects appear whenever difference equations are iterated in a multispecies dynamical system and can dramatically alter the nature of species interactions, even turning direct competitors into indirect mutualists (Vandermeer et al. 1985). Nevertheless, Eq. 1 fails to represent an important class of complex interactions in nature. Species can alter the pairwise interactions of other species, not by affecting numbers, but by directly affecting the interaction coefficients. For example, a plant species can alter the strength of a predator-prey interaction by providing cover for the prey. A dominant competitor can alter the spatial and/or temporal activity of two subordinate competitors, instantaneously changing their direct relationship with each other (Ulanowicz 1972, Miller and Kerfoot 1987, Strauss 1991, Worthen and Moore 1991).

To model this kind of complex interaction, a second set of simulations was run with three-dimensional interaction matrices. Each element of that matrix, α_{hij} , refers to the effect of species j on species i in the presence of species h . As before, the elements are random numbers uniformly distributed between 0 and 2 with the exception of self-effects (α_{hii}), which are unity. The three-dimensional matrix is then collapsed into a two-dimensional matrix by taking a weighted average of the 10 elements governing every pairwise interaction:

$$\alpha_{ij} = \sum_{h=1}^S p_h \alpha_{hij}, \quad (2)$$

where p_h is the relative proportion of species h in the patch. The two-dimensional matrix must be recalculated for every iteration of the difference equations because the relative proportions of species in the patch are always changing. Here, then, is another way to

represent the basic idea that *pairwise species interactions depend on the community in which the species are embedded*.

For most sets of parameter values, simulation runs were performed on a sample of 10 randomly generated interaction matrices. The two-dimensional matrices are labelled **M1–M10** and the three-dimensional matrices are labelled **M11–M20**. Using a sample of interaction matrices allows general trends to be distinguished from the idiosyncracies associated with any particular matrix.

To understand the effects of complex interactions per se, without the additional effects of metacommunity structure, numerous simulations were run for single patches in which the initial species proportions (p_1, p_2, \dots, p_S) and total density of all species (N) was specified.

Patch-level selection

To explore the effects of complex interactions on natural selection at the patch level, one species in the metacommunity was designated as either "detrimental" or "beneficial" to the productivity and/or extinction of the entire patch. Specifically, each patch was censused after the l th iteration of the difference equations, just before dispersal into the global pool. The densities of all species in the patch were then reduced by a function $e(x)$, where x is the proportion of the designated species in the patch. The function $e(x)$ can be interpreted as a probability of patch extinction or as a term governing the relative productivity of the patches. The specific functions used for $e(x)$ are provided in the *Results* section.

To summarize, a simulation run consisted of the following steps. (1) Parameters of the logistic equation are defined and the interaction matrix is filled with a set of random numbers (which remain constant during the course of the simulation); (2) Parameters of the metacommunity are defined, including the initial global proportion of species, the numbers of individuals colonizing each patch, and the background density whereby all species enter all patches; (3) The dynamics of the metacommunity are examined by monitoring changes in global species proportions over C cycles of colonization and dispersal, along with the variance of local species proportions among patches just prior to dispersal; (4) The dynamics of single patches with specified initial conditions are examined in selected cases; (5) Response to patch-level selection is examined by applying a selection function ($e(x)$) that governs the contribution of each patch to the global pool of dispersers.

RESULTS

Two-dimensional interaction matrices

The dynamics of metacommunities governed by two-dimensional interaction matrices can best be intro-

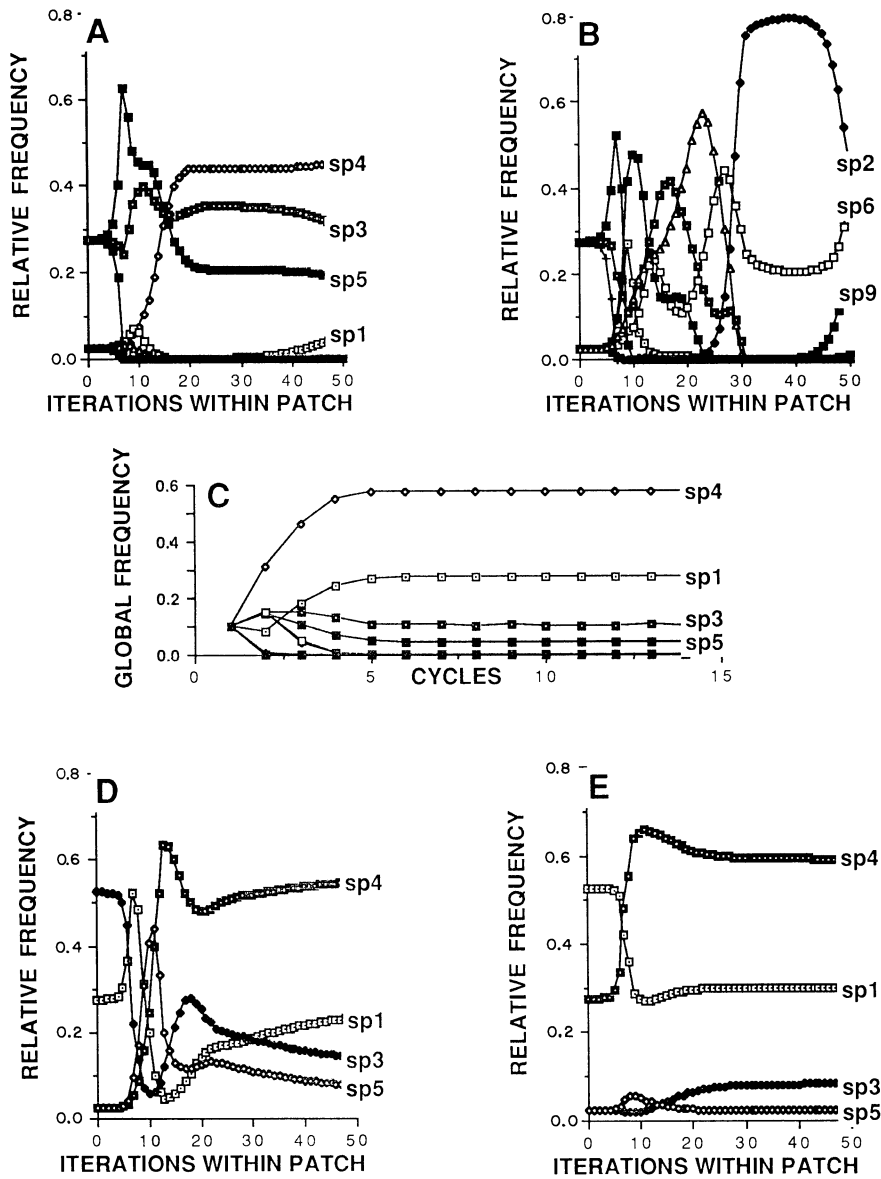


FIG. 1. Local and global dynamics of a metacommunity governed by interaction matrix $M7$ when each patch is colonized by $N = 3$ individuals and background density (B) = 0.1. Parts (A) and (B) show diverging trajectories of two patches drawn from a global pool in which all species are present in equal proportions. Part (C) shows how the composition of the global pool changes over 15 cycles of colonization, interaction, and dispersal. Parts (D) and (E) show the converging trajectories of two patches drawn from the global pool at its equilibrium.

duced with an example. Figs. 1A and B portray two local patches that are governed by the same parameter values (carrying capacity, $K = 1000$; rate of increase, $R = 2$; interaction matrix $M7$), but which differ in their initial species proportions. The two patches were colonized by drawing $N = 3$ individuals at random from a global pool in which all species were equally represented, and then allowing all other species to enter the patch at a background density of $B = 0.1$. Both patches take off on different trajectories through S -space and have radically different species compositions after 50 iterations of the difference equations. Neither reaches

an equilibrium during this time, and in both cases the species that are most abundant at colonization do not necessarily prevail within the patch.

The effect of interactions within patches on variation between patches is shown in Fig. 2. The open circles represent the variance in the proportion of each species among a sample of 100 patches (y axis) as a function of its average frequency in the metacommunity (x axis) after 50 iterations of the difference equations. Only 7 of the 10 species are represented because 3 species have declined to the background density in all patches and have zero variance. For comparison, the solid squares

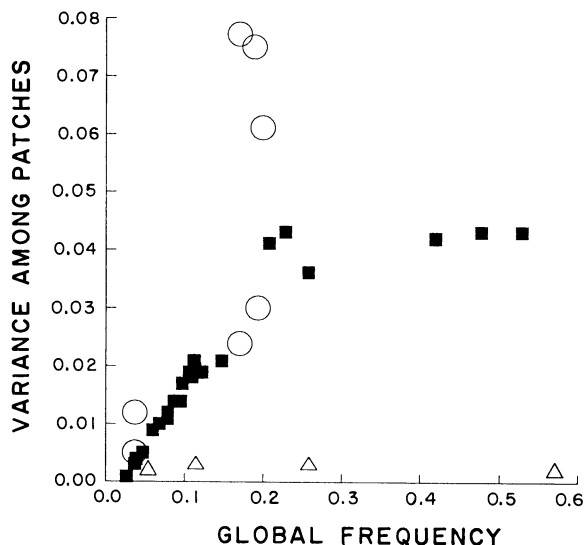


FIG. 2. The effect of interactions on variation among patches in a metacommunity governed by interaction matrix **M7**. ■ shows variance in species proportions among patches as a function of global frequency immediately after colonization. ○ shows variance among patches after interactions for a sample of 100 patches drawn from a global pool in which all species are initially present in equal proportions. △ shows variance among patches after interactions for a sample of 100 patches drawn from a global pool at its equilibrium.

represent the variance that would be expected from sampling error alone. These were generated in separate simulation runs by varying the relative proportion of species in the global pool and calculating variance among patches just after colonization and before deterministic interactions. Returning to the open circles, interactions within patches maintain variation between patches for all seven species and increase variation to above-random levels for three species.

Thus it appears that complex interactions can magnify the cloud of variation that is initiated by sampling error, exactly as described verbally in the *Introduction*. However, the simulations so far do not represent an equilibrium situation. The global pool during the next cycle will be biased in favor of the species that were most abundant, on average, in the local patches just prior to dispersal, which in turn will influence the initial composition of the next "generation" of patches. Fig. 1C shows the relative proportion of species in the global pool over 15 cycles of colonization, interaction, and dispersal. The global community soon reaches a steady state in which species 1, 3, 4, and 5 are most prevalent. Note that these are the same species that prevailed in the local patch shown in Fig. 1A.

Figs. 1D and E portray two local patches that were drawn at random from the equilibrium global pool. They do not diverge but rather converge towards the same local equilibrium. The open triangles in Fig. 2 show the same result for 100 patches drawn at random from the equilibrium global pool. Deterministic inter-

actions no longer maintain or expand variation among patches but rather reduce it to near zero.

The results of this single example can be summarized as follows: The interactions among species are sufficiently complex that initial composition is an important determinant of a local patch's trajectory through *S*-space. However, some regions of *S*-space attract more local patches than others, and the species composition of the global pool ultimately becomes centered on one of these more attractive regions. Thereafter, the cloud of variation that is initiated by sampling error falls largely within a single domain of attraction, and the effect of interactions is mainly to collapse variation between patches. At global equilibrium, metacommunity structure adds remarkably little to the dynamics of single patches.

With this example in mind, we can now systematically alter the various parameters of the model.

The interaction matrix.—The above exercise was repeated for 10 randomly generated interaction matrices (**M1**–**M10**) with other parameter values held constant ($K = 1000$, $R = 2$, $N = 3$, $B = 0.1$, $I = 50$, $C = 60$). In nine cases the global community became centered on a single domain of attraction with 2–4 coexisting species. The effect of interactions was to reduce variation caused by sampling error to near zero. The one exception (**M9**) is worth analyzing in detail. Five species (1, 2, 4, 5, and 10) were maintained at global frequencies of 0.464, 0.015, 0.021, 0.052, and 0.448, respectively. The subset of matrix **M9** that pertains to these species is shown in Table 1. Examination of the coefficients reveals two stable local equilibria, one composed of species 1 and 10 and the other composed of species 2 and 4. Given the composition of the global pool, most patches are colonized by species 1 and 10 and proceed directly to that local equilibrium (Fig. 3A). Species 5 can outcompete the 1–10 combination if it is sufficiently abundant (e.g., if it is one of the initial colonists) but itself is vulnerable to the 2–4 combination. However, the patches do not always reach a local equilibrium before blending back into the global pool. For example, patches colonized by a single individual of species 1, 5, and 10 persist long enough for species 5 to largely replace species 1 and 10, but not long enough for species 2 and 4 to replace species 5

TABLE 1. Relevant portion of interaction matrix **M9**, which allows five species to coexist in the global community. See *Results: The interaction matrix* and Fig. 3 for additional explanation.

Species <i>i</i>	Species <i>j</i>				
	1	2	4	5	10
1	1.00	1.89	0.99	1.16	0.02
2	1.94	1.00	0.60	0.41	1.29
4	1.73	0.44	1.00	0.23	0.13
5	1.04	0.79	1.73	1.00	0.00
10	0.04	1.53	0.62	1.33	1.00

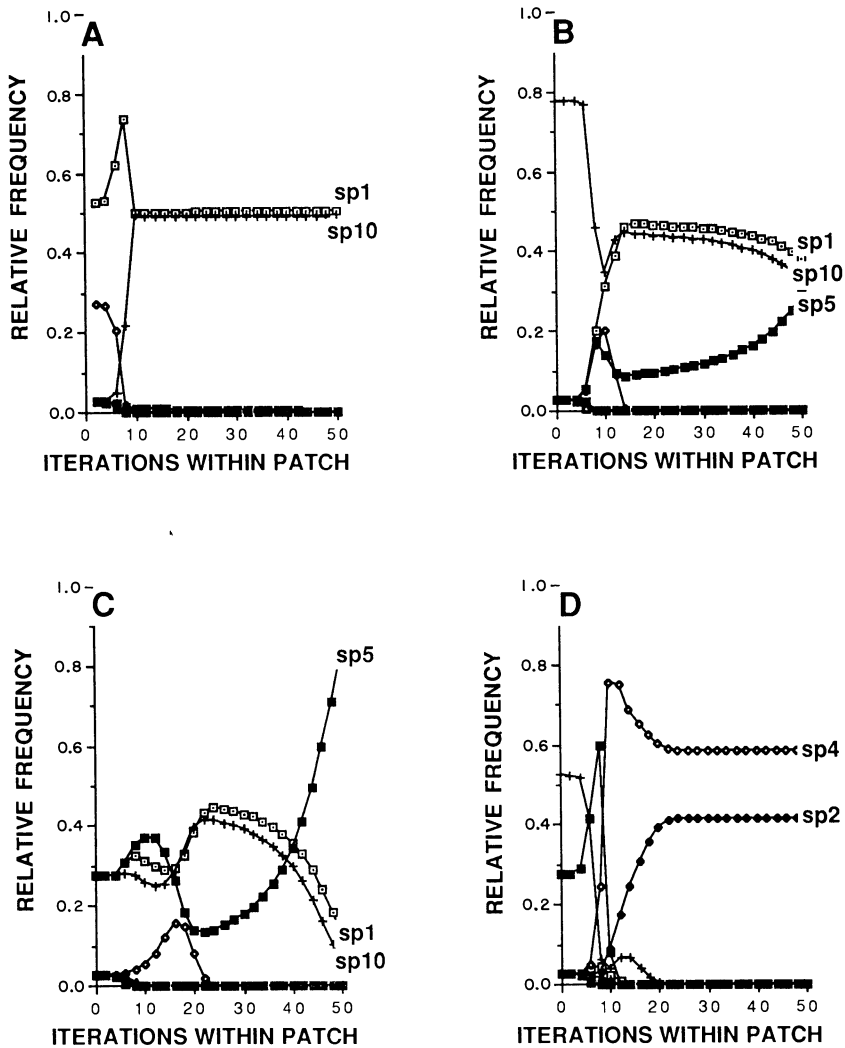


FIG. 3. Divergent local dynamics of patches drawn from a global pool at its equilibrium in a metacommunity governed by interaction matrix **M9**.

(Fig. 3C). Patches that are colonized by one individual of species 5 and two individuals of species 10 do succumb to the 2–4 combination because species 5 replaces species 10 faster in the absence of species 1 (Fig. 3D). Although the trajectories represented by Figs. 3B–D are not common, they are sufficiently frequent to maintain species 2, 4, and 5 in the global pool above their background density. The net effect of local interactions is to increase variance among patches by a factor of 8 for species 2 and by a factor of 4 for species 4. Variance declines below colonization values for species 1, 5, and 10 but remains well above zero.

Patch duration (I).—Since local patches do not quickly reach equilibrium, the relative proportions of species that enter the global pool can be expected to change with patch duration. The effect of patch duration was examined by comparing matrices **M1** through **M10** at $I = 5$, $I = 15$ and $I = 50$ with other parameters held constant ($K = 1000$, $R = 2$, $N = 3$, $B = 0.1$, $C = 60$).

At $I = 5$, all 10 species were maintained at approximately equal frequencies in the metacommunity for all interaction matrices. This is because species densities are so far below carrying capacity during the first five iterations that the interaction terms have negligible effects on growth rates, which instead are governed by the constant value R . Thus, for very small values of I the simulations converge on a nearly neutral model in which all species have the same minimal input (represented by B) and growth rates that are nearly equal (represented by R , slightly modified by the interaction terms).

When $I = 15$, the interaction terms have become important determinants of species abundance, and yet most local patches are far from equilibrium. Surprisingly, for all 10 interaction matrices, the global equilibrium that results when $I = 15$ is qualitatively similar to the global equilibrium that results when $I = 50$. The same species persist in roughly the same proportions.

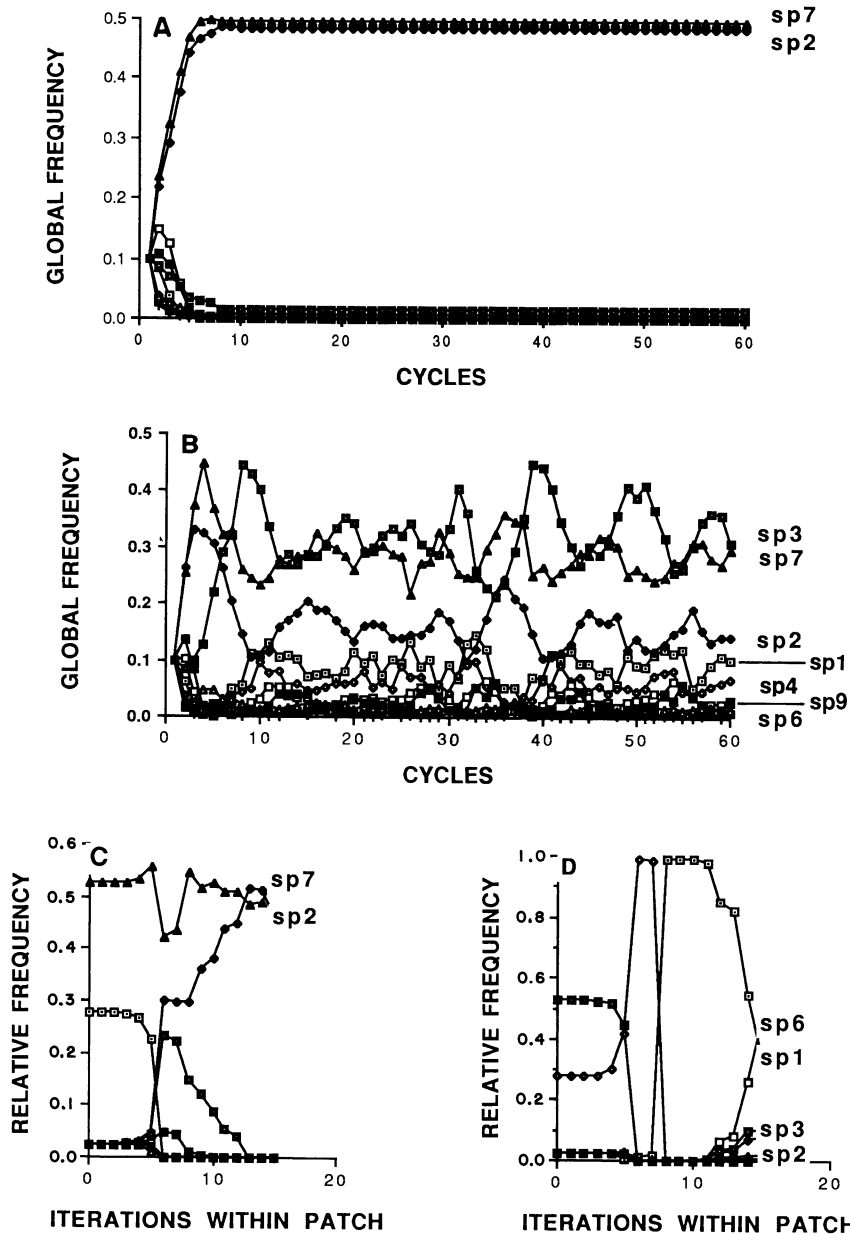


FIG. 4. Global dynamics of a metacommunity governed by interaction matrix M_4 when rate of increase $R = 2$ (A) and when $R = 3$ (B). Parts (C) and (D) show the dynamics of two local patches when $R = 3$.

Rate of increase (R).—High rates of increase can have dramatic effects on the dynamics of single patches by causing species numbers to overshoot equilibria, resulting in oscillating or chaotic fluctuations (May 1989). The effect of high rates of increase on metacommunity dynamics can best be introduced with an example. For parameter values $K = 1000$, $R = 2$, $N = 3$, $B = 0.1$, and $I = 15$, matrix M_4 yields a metacommunity consisting of species 2 and 7 in equal abundance, with all other species at frequencies of $< 1\%$ (Fig. 4A). Fig. 4B shows the metacommunity dynamics of matrix M_4 when R is increased from 2 to 3 and all

other parameters are held constant. Now seven species coexist globally at appreciable frequencies. Figs. 4C and 4D show a sample of local patches that were drawn from the global pool during the 20th cycle. Far from converging on the same local equilibrium, the species composition of each patch at $I = 15$ now depends radically on its initial composition at $I = 0$. When variance in the frequency of each species is calculated from a sample of 100 patches, the average variance after interactions is over five times greater than the corresponding value at colonization.

At least three features of this example are worth

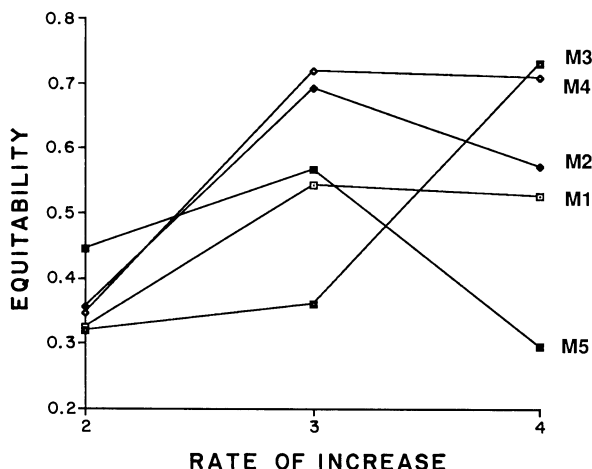


FIG. 5. Equitability index E as a function of rate of increase R for metacommunities **M1**–**M5**. $E = 0$ when the entire community is composed of a single species, and $E = 1$ when all 10 species exist in equal proportions (see Krebs 1978: 456 for method of calculation).

stressing. First, increasing R qualitatively changes the effects of species interactions on variance among patches, since the cloud of variation shrinks when $R = 2$ and expands when $R = 3$. Second, increasing R dramatically increases the number of species that coexist in the metacommunity—from two to seven. Third, although the global frequency of species does not equilibrate during 60 cycles of colonization and dispersal, each species fluctuates within a relatively narrow range. To test for the existence of stabilizing forces, a perturbation experiment was performed on the metacommunity after the 19th cycle, in which the frequency of each species was first lowered to 0.001 and then raised to twice its observed frequency on the 19th cycle. In every case the frequencies increased from the lowered values and decreased from the raised values. Thus, the unstable and widely varying dynamics of single patches combine to form a relatively stable dynamic at the metacommunity level.

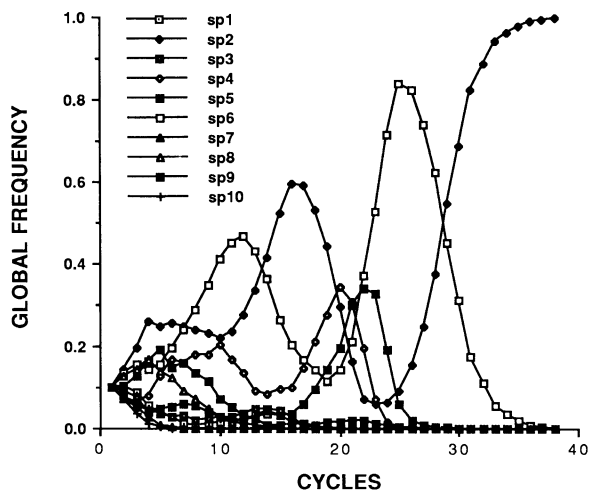
To determine the generality of these patterns, simulations were run for matrices **M1**–**M5** at $R = 2$, $R = 3$, and $R = 4$, with other parameters held constant ($K = 1000$, $I = 15$, $N = 3$, and $B = 0.1$, $C = 60$). Increasing R usually increases both variance among patches and the number of species that coexist in the metacommunity, represented as the equitability index E in Fig. 5. Matrix **M5** constitutes an exception in which the metacommunity became dominated by a single species at $R = 4$.

Numbers of colonizing individuals (N) and background density (B).—Intuitively, increasing variation between patches at colonization should have the effect of extending the initial cloud of variation to more domains of attraction, thereby increasing the potential of deterministic interactions to expand the cloud. The quantitative effects of variance at colonization were

explored for matrices **M1**–**M10** by running simulations at $N = 2, 3, 5, 10$, and 20 for values of $B = 0$ (patches closed after initial colonization) and $B = 0.1$. All other parameters were held constant ($K = 1000$, $I = 15$, $R = 2$).

When all species are allowed into every patch at a low background density ($B = 0.1$), the value of N has only minor effects on global dynamics. This is not surprising, since we know from *The interaction matrix*, above, that the cloud of variation usually becomes centered on a single domain of attraction when N is as low as three.

When $B = 0$, high values of N usually give results that are similar to $B = 0.1$, but low values of N can radically alter global dynamics. Matrix **M7**, whose dynamics for $B = 0.1$ and $N = 3$ are shown in Fig. 1, provides an interesting example. The relevant portion of the matrix and the global dynamics for $B = 0$ and $N = 2$ are shown in Fig. 6. The metacommunity soon becomes dominated by species 2, 4, 6, and 9, whose frequencies oscillate with increasing amplitude until only species 2 remains. To understand these oscillations, first consider a metacommunity composed entirely of species 2 and 6 in proportions p and $(1 - p)$,



		Species j			
		2	4	6	9
Species i	2	1.00	1.83	0.33	1.99
	4	1.03	1.00	1.54	1.72
	6	0.83	1.12	1.00	0.28
	9	0.15	1.45	1.99	1.00

FIG. 6. Global dynamics of metacommunity governed by matrix **M7** when each patch is colonized by $N = 2$ individuals and background densities (B) are zero. The metacommunity becomes dominated by a single species (sp2). Parameter values of $N = 3$ and $B = 0.1$ completely alter the global dynamics, as shown in Fig. 1.

respectively. A fraction p^2 of the patches will be colonized entirely by species 2 and will grow to $K = 1000$. Similarly, a fraction $(1 - p)^2$ of the patches will be colonized entirely by species 6 and also will grow to $K = 1000$. The remaining $2p(1 - p)$ patches will be colonized by one individual of each species whose interactions are governed by the matrix terms $\alpha_{26} = 0.33$ and $\alpha_{62} = 0.83$, which leads to a stable equilibrium in which $N_2 = 923$ and $N_6 = 234$. After dispersal, the frequency of species 2 in the metacommunity will be

$$p' = [p^2(1000) + 2pq(923)]/[p^2(1000) + 2pq(1157) + (1 - p)^2(1000)].$$

Notice that p' always exceeds p because the mixed patches always produce an excess of species 2, whereas all other aspects of the process are neutral with respect to the frequency of types. In other words, *species 2 excludes species 6 from the metacommunity despite the fact that the two species coexist indefinitely within every mixed patch*. The process is similar to population genetic models of meiotic drive, in which the "patches" are diploid genotypes "colonized" by $N = 2$ alleles (e.g., Hartl and Clark 1989: 190).

Inspecting the other interaction terms between species 2, 4, 6, and 9 reveals that species 2 is excluded within patches by species 4 and 9, which in turn are excluded by species 6. The overall metapopulation dynamic consists of species 6 increasing at the expense of 4 and 9, thereby making itself vulnerable to species 2, which itself achieves prominence only to succumb to species 4 and 9. The dynamics become even more complex when $N = 3$ but then revert at $N = 5$ to a pattern similar to that in Fig. 1, in which species 1 and 4 are the dominant species that coexist both locally and globally. It is striking that the metacommunity in Fig. 1 owes its stability and its particular species composition to the fact that the patches are open to colonization by more than a few individuals.

The major results for two-dimensional matrices can be summarized as follows: At low rates of increase ($R = 2$), the species composition of the dispersal pool usually becomes "centered" over a single basin of attraction. Although sampling error produces a cloud of variation among patches, deterministic interactions have the effect of shrinking the cloud as each patch converges on the same local equilibrium. When sensitivity to initial conditions is increased (e.g., by changing R from 2 to 3), the cloud of variation produced by sampling error no longer can "fit" within a single basin of attraction. Interactions then have the effect of maintaining and magnifying the cloud of variation as patches follow diverging trajectories. In addition, increasing sensitivity to initial conditions often, but not always, increases the biodiversity of the metacommunity.

Three-dimensional interaction matrices

The three-dimensional matrices are intended to represent the fact that pairwise species interactions can be

directly influenced by other species in the local community. Mathematically, replacing the constants of the two-dimensional matrices with linear functions of patch composition greatly increases sensitivity to initial conditions, even when the rate of increase is low ($R = 2$). The effects on local and global dynamics are shown for one metacommunity (M13) in Fig. 7. At the global level, 8 out of the 10 species are maintained well above background density in proportions that appear relatively stable (Fig. 7A). Unlike the global pattern in Fig. 1, which merely reflects the dynamics of a single local equilibrium, the global pattern in Fig. 7A reflects many different trajectories at the patch level, two of which are shown in Figs. 7B and C. As a result, the cloud of variation that is initiated by sampling error is maintained, and in some cases magnified, by local interactions.

Although variance in the proportion of species among patches provides a crude measure of the cloud of variation, it is also useful to observe the actual shapes of the distributions and the correlation structure that develops as the result of species interactions. Fig. 8 shows how the most abundant species (sp5) and the rarest species that is maintained above background density (sp7) are distributed among patches just prior to dispersal. Both distributions are bimodal, implying that the species thrive in some patches and wither in others, depending on the background community. Even species 7 achieves high densities in a small proportion of patches. The relatively stable global species proportions are an average of these very different local outcomes. Table 2 shows that local proportions are highly intercorrelated, with nine positive and eighteen negative associations that are significant at the .05 level for a sample of 100 patches (Bartlett chi-square test).

The results of this single example can be summarized as follows: By increasing sensitivity to initial conditions, the three-dimensional matrix has much the same effect as increasing R from 2 to 3 in two-dimensional matrices. Even after the composition of the dispersal pool has achieved a rough equilibrium, the cloud of variation created by sampling error does not fall within a single domain of attraction, and is therefore preserved and magnified by deterministic interactions.

With this example in mind, we can now systematically alter the various parameters of the model.

The interaction matrix.—The above exercise was repeated for 10 randomly generated three-dimensional interaction matrices (hereafter referred to as M11–M20) with other parameter values held constant ($K = 1000$, $R = 2$, $N = 3$, $B = 0.1$, $I = 15$, $C = 60$). In one case (M19) the global pool became centered on a single domain of attraction in which only two species coexisted, similar to the results described in *Two-dimensional interaction matrices: The interaction matrix*, above. The remaining nine cases resembled the example cited above. In particular:

a) Global species diversity is considerably greater in

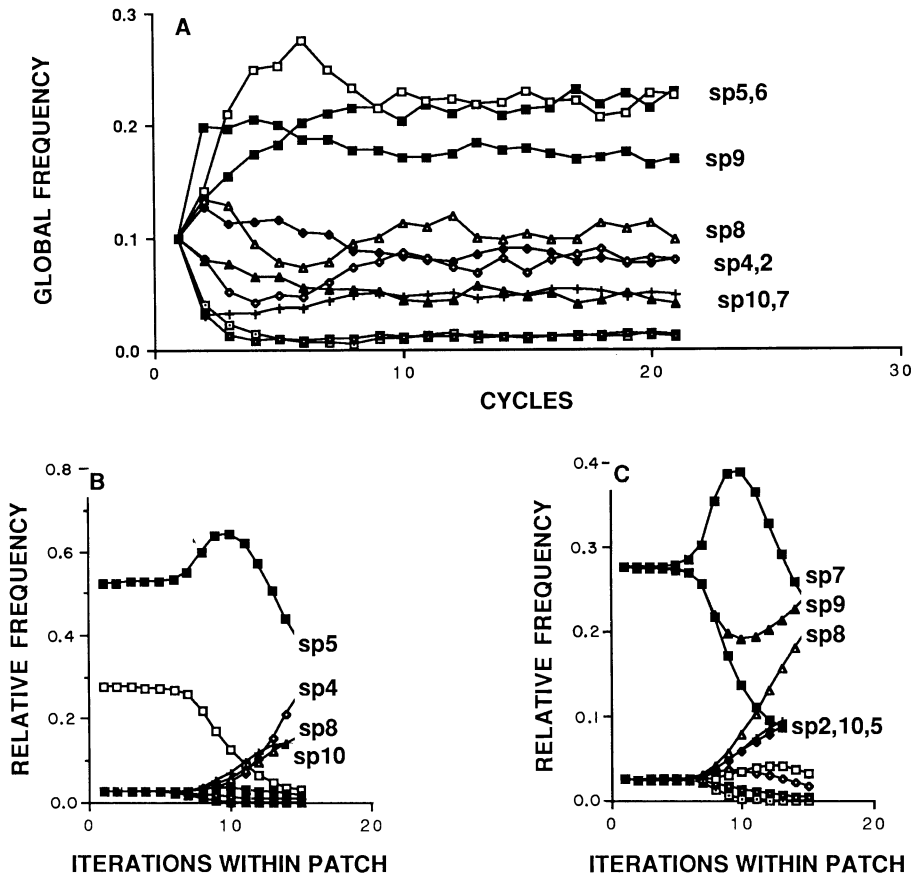


FIG. 7. Global (A) and local (B and C) dynamics of a metacommunity governed by three-dimensional interaction matrix M13. Many species coexist globally, and local dynamics are divergent.

metacommunities governed by three-dimensional matrices. The average equitability index for metacommunities governed by M11–M20 is 0.68, as opposed to 0.41 for metacommunities governed by M1–M10.

b) Global dynamics are relatively stable. Coexisting species maintain characteristic rank orders during simulation runs and return to the same rank order when global frequencies are perturbed. At a finer scale, however, the small fluctuations in global frequency observed in Fig. 7A are characteristic and show no signs

of damping, even after 60 cycles of colonization and dispersal.

c) Global dynamics do not reflect a single local equilibrium but rather a diversity of trajectories at the patch level.

d) The effect of species interactions is almost always to maintain variation between patches and frequently to increase it above colonization levels (Fig. 9). Species frequently thrive in some patches and wither in others, creating bimodal distributions of abundance. Species

TABLE 2. Pearson correlation matrix relating species proportions in a sample of 100 patches from a metacommunity governed by matrix M13. Correlations in bold type are significantly different from zero at the .05 level or below.

Species	sp1	sp2	sp3	sp4	sp5	sp6	sp7	sp8	sp9	sp10
sp1	1.0									
sp2	0.10	1.0								
sp3	0.03	-0.11	1.0							
sp4	-0.08	-0.32	0.30	1.0						
sp5	-0.27	-0.68	-0.04	0.20	1.0					
sp6	-0.17	0.12	-0.34	-0.52	0.02	1.0				
sp7	-0.05	0.45	-0.05	-0.21	-0.46	-0.40	1.0			
sp8	0.37	-0.23	0.13	-0.08	-0.32	-0.41	0.07	1.0		
sp9	-0.23	0.55	-0.12	-0.55	-0.46	0.25	0.43	-0.21	1.0	
sp10	-0.13	-0.34	0.27	0.63	0.23	-0.50	-0.12	-0.03	-0.52	1.0

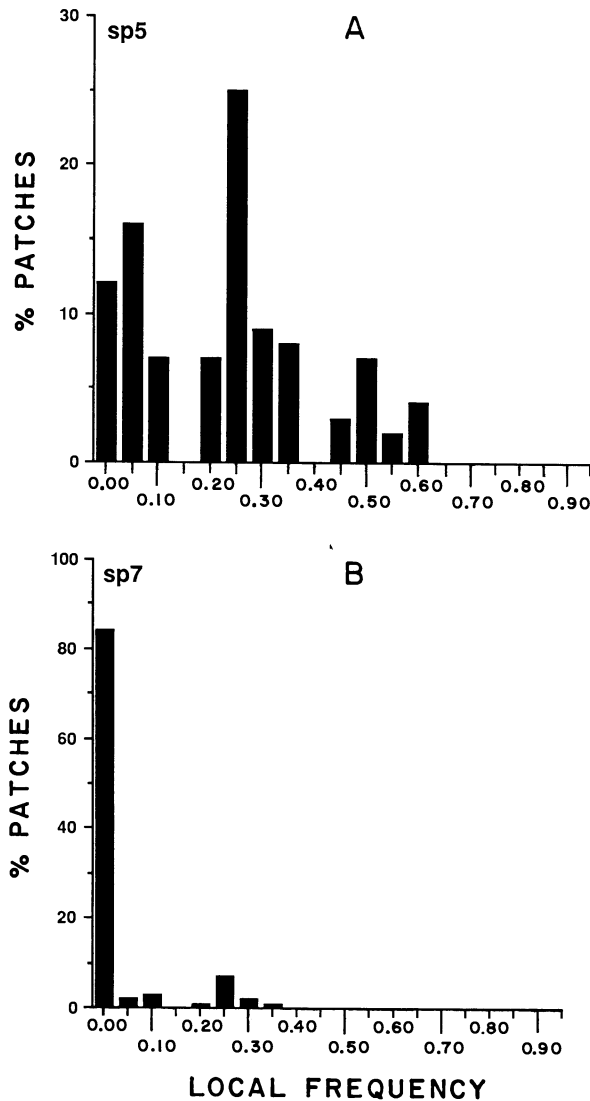


FIG. 8. The relative proportions of species 5 (A) and species 7 (B) in a sample of 100 patches from the metacommunity represented in Fig. 7. The y axis gives the proportion of patches in which the species exists at a given range of frequencies after interactions. Species 5 is globally the most common species, but nevertheless is rare or absent in a large proportion of patches. Species 7 is globally the least common species that is maintained above background density, but nevertheless flourishes in a small proportion of patches.

that are rare globally nevertheless achieve high densities in a small proportion of patches. Interactions create a correlation structure among species that is absent at colonization.

Patch duration (I).—The effect of patch duration was examined by comparing matrices **M11**–**M20** at $I = 15$ and $I = 50$ with other parameters constant ($K = 1000$, $R = 2$, $N = 3$, $B = 0.1$; $I = 5$ was not examined for reasons discussed above [see *Two-dimensional inter-*

action matrices: Patch duration]. In two cases metacommunities that were diverse at $I = 15$ collapsed into simpler metacommunities at $I = 50$, changing the equitability index from 0.73 to 0.38 for **M11** and from 0.74 to 0.30 for **M15**. The maintenance of global species diversity in these metacommunities evidently required transient local dynamics that disappeared when patches were allowed to persist. The remaining eight metacommunities retained the same global species diversity (average change in the equitability index = 0.037) and in most cases the same species composition (average change in global species proportion = .024). Increasing patch duration dramatically altered the rank order of species in only one case (in **M17**, sp7 changed from rank 6 to rank 1). To summarize, increasing patch duration usually had little effect on the results outlined in *The interaction matrix* (above) for $I = 15$ but occasionally had dramatic effects.

Rate of increase (R).—For metacommunities governed by two-dimensional matrices, high R values increase sensitivity to initial conditions, usually increasing both global species diversity and variance among patches, although in one case the metacommunity collapsed to a single species (see *Two-dimensional interaction matrices: Rate of increase*, above). Three-di-

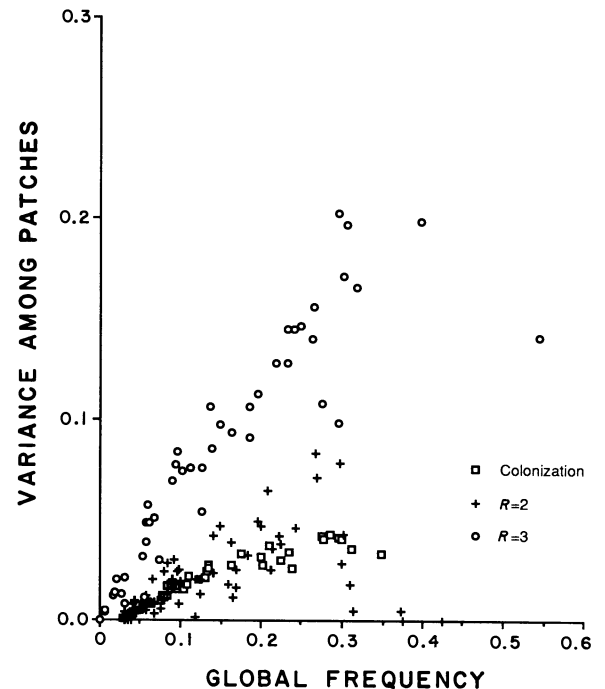


FIG. 9. Variance in the proportion of species i among patches as a function of its global frequency for 10 metacommunities governed by three-dimensional interaction matrices. \square = variance after colonization; $+$ = variance after interactions when $R = 2$; and \circ = variance after interactions when $R = 3$. Variation among patches is usually maintained and frequently increased by complex interactions within patches.

mensional matrices provide another mechanism for increasing sensitivity to initial conditions, even when R values are low (*The interaction matrix*, above). The joint effect of high R values and three-dimensional matrices was examined by comparing matrices **M11–M20** for $R = 2$ vs. $R = 3$ and other parameters held constant ($K = 1000$, $I = 15$, $N = 3$, $B = 0.1$). Increasing R substantially *decreased* global species diversity in four cases and had a trivial effect in the remaining six cases. In three cases (**M11**, **M14**, **M19**) the global pool became centered on a single domain of attraction with 1–2 coexisting species. For the remaining seven cases, increasing R substantially *increased* variance among patches, as shown in Fig. 9.

Numbers of colonizing individuals (N) and background density (B).—When metacommunities are governed by two-dimensional matrices, the cloud of variation created by sampling error usually falls within a single domain of attraction when $R = 2$, $N = 3$ and $B = 0.1$. Increasing N above this value therefore has little effect on local and global dynamics (*Two-dimensional interaction matrices: Rate of increase*, above). When metacommunities are governed by three-dimensional matrices at the same values of R , N , and B , the cloud of variation usually spans more than one domain of attraction, causing the trajectories of patches to diverge rather than converge (see *The interaction matrix*, above). As we increase the number of individuals colonizing each patch, the cloud of variation caused by sampling error should shrink until ultimately it falls within a single domain of attraction. If local dynamics are sufficiently sensitive to initial conditions, however, even large values of N will provide sufficient initial variation to be magnified by complex interactions. The quantitative effects of variance at colonization were explored for matrices **M11–M20** by running simulations at $N = 3, 5, 10$, and 20 for values of $B = 0$ and $B = 0.1$. All other parameters were held constant ($K = 1000$, $I = 15$, $R = 2$, $C = 60$). Results can be summarized as follows.

- a) As for metacommunities governed by two-dimensional matrices, the value of B has little effect on global dynamics for larger values of N .
- b) Global species diversity declined with increasing values of N . Average equitability index (E) is 0.68 when $N = 3$ and 0.47 when $N = 20$.
- c) At $N = 20$, 6 of the 10 metacommunities became centered on a single domain of attraction, so that interactions eliminated variation between patches. Variance was maintained in the other four metacommunities and sometimes magnified by as much as a factor of 10.
- d) In three metacommunities, the global dynamics became *more* oscillatory as N increased. This is probably because the local dynamics were themselves oscillatory, and high values of N caused patches to be initiated in phase with each other.

Patch-level selection

A pair of examples will introduce the effects of complex interactions on patch-level selection. Consider the metacommunity in Fig. 1 (**M7**) in which four species coexist both globally and within each patch. Assume that species 4 (the most common species) increases the probability that the entire patch will go extinct. Mathematically, patch-level extinction is incorporated into the model by censusing each patch just prior to dispersal and setting the density of all species to zero with a probability $e(p_4) = ap_4$, where a is a constant and p_4 is the frequency of species 4 in the patch (extinction probability is set to one if $ap_4 > 1$).

For two reasons, patch-level extinction does not significantly alter the dynamics of the metacommunity represented by Fig. 1, regardless of the value of a . First, the cloud of variation that is created by sampling error during the colonization phase is collapsed by interactions to a much smaller cloud just prior to dispersal. Since patches are virtually identical, the extinction of some and survival of others does not bias the composition of the global pool. Second, even if extinctions did reduce the proportion of species 4 in the global pool, stabilizing forces within patches would return species 4 to the same local equilibrium prior to the next episode of extinction. Thus, patch-level selection is ineffective in this simulation run. More generally, it is possible for patches to suffer a high rate of extinction caused by the activities of species within the patches, without altering the basic dynamics of the metacommunity.

Now consider the metacommunity represented by Fig. 7 (**M13**), in which the global dynamics reflect a diversity of patch trajectories. As for the previous example, assume that the most common species (species 5 in this case) increases the probability of patch extinction according to the function $e(p_5) = ap_5$. Fig. 10A shows the effect of patch-level extinction on the global frequency of species 5 for various values of a . The initial composition of the metacommunity was taken from the the last cycle of Fig. 7; i.e., the metacommunity was assumed to be at its equilibrium before patch-level extinction was applied.

In contrast to the metacommunity represented by Fig. 1, patch-level extinction now reduces the frequency of species 5 to a new equilibrium that depends on the value of a . For example, when $a = 2$ the average patch at the beginning of the simulation contains species 5 at a frequency of $p_5 = 0.22$ and therefore goes extinct with a probability $e(p_5) = 0.44$. Species 5 rapidly declines to a new global equilibrium at $p_5 = .064$, less than a third of its former value. A much smaller proportion of patches go extinct during each cycle ($\approx 13\%$), yet this is sufficient to maintain the new equilibrium.

In addition to reducing the frequency of species 5, patch-level extinction also restructures the entire metacommunity, as shown for $a = 2$ in Fig. 10B. The rank

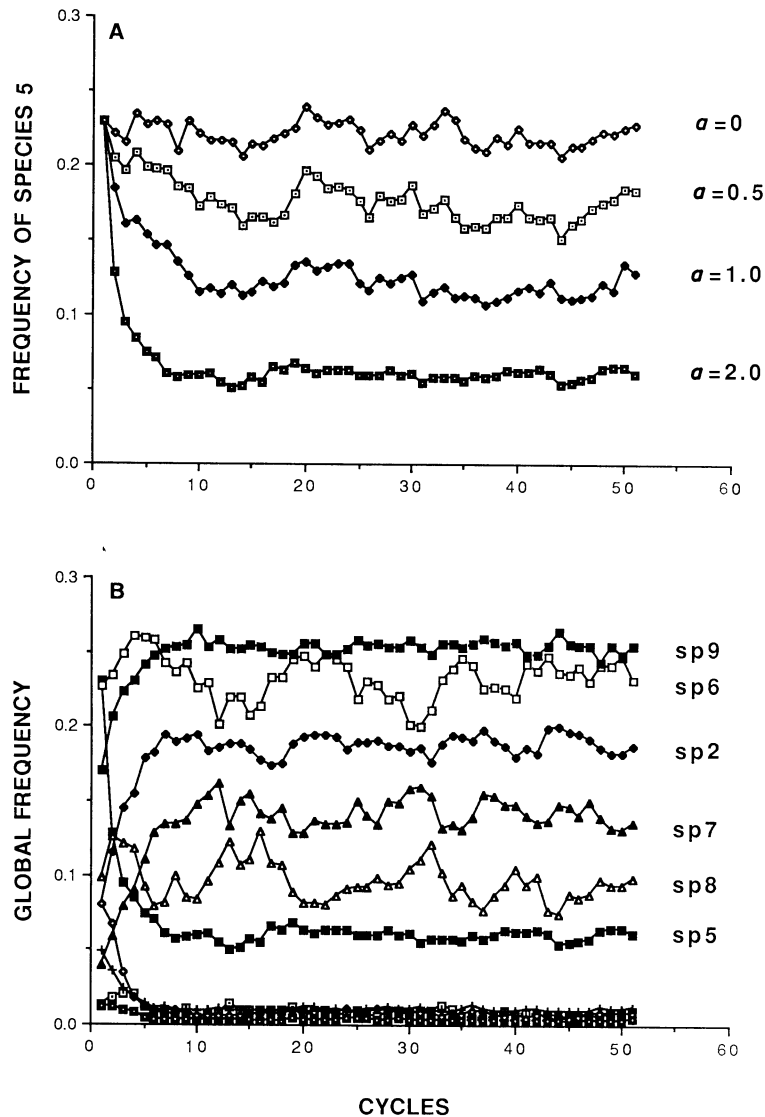


FIG. 10. Patch-level selection in a metacommunity governed by three-dimensional matrix **M13**. The probability of patch extinction (e) is directly proportional to the frequency of species 5 (p_5) according to the function $e(p_5) = ap_5$. Part (A) shows the effect of patch-level selection on the global frequency of species 5 for various values of a . Part (B) shows the global dynamics of the entire metacommunity when $a = 2$, which can be compared with Fig. 7 when $a = 0$. Patch-level selection against species 5 alters the global frequency of many other species because of the correlation structure shown in Table 2.

order of species is substantially altered (compare Fig. 10B with Fig. 7A) and two species (4 and 10) have declined to background densities.

Patch-level selection is effective in this example for several reasons. First, variation in p_5 ensures that extinction removes a biased sample of patches, leaving a reduced frequency of species 5 in the global pool. Second, extinction operates not only against species 5, but against all species that correlate positively with species 5 (see Table 2). Third, the correlation structure in Table 2 reflects an underlying set of causal relationships in which species 5 is facilitated by some species and inhibited by others. By differentially removing species 5 and its associates, patch-level extinction leaves

behind a set of background communities that are less conducive to the growth of species 5 during the next cycle. Thus, interactions within patches do not necessarily return species 5 to its original frequency, as they do for the metacommunity represented by Fig. 1. We begin with a virulent species that drives local communities extinct, and we end with a set of local communities that drive the virulent species extinct.

To explore the generality of this result, a number of additional simulations were run on metacommunities governed by three-dimensional matrices.

Intensive analysis of a single metacommunity.—To see if all species in metacommunity **M13** are as sensitive to patch-level extinction as species 5, the follow-

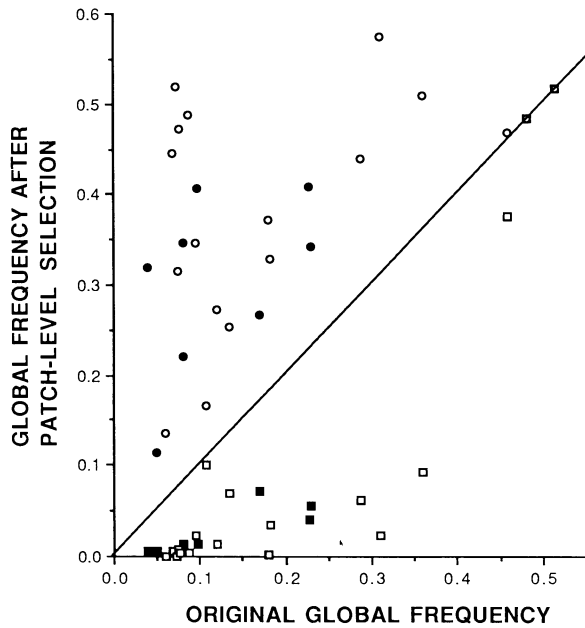


FIG. 11. The effect of patch-level selection in 10 metacommunities governed by three-dimensional interaction matrices (M11–M20). The global frequency of a given species after patch-level selection is related to its global frequency before selection. Points that fall above the diagonal line have increased in frequency, while points that fall below the diagonal line have declined. Species either increased (circles) or decreased (squares) the probability of patch survival. The solid symbols represent all species in a single metacommunity (M13) that are maintained above background density. The open symbols represent two species from each of 10 metacommunities.

ing procedure was employed on each species in turn. First, based on the equilibrium global frequency of that species without patch-level extinction (p_i), a value of a was chosen such that $ap_i = 0.5$. Second, patches containing species i were selected *against* according to the function $e(p_i) = ap_i$, as outlined above. The chosen value of a ensures that roughly half the patches go extinct at the beginning of the simulation. Third, patches containing species i were selected *for* according to the function $e(p_i) = 1 - ap_i$, where $e(p_i) = 0$ if $ap_i > 1$. As for step two, roughly half the patches go extinct at the beginning of the simulation, but in this case species i prevents extinction rather than causing it. Fig. 11 shows the equilibrium global frequency after patch-level selection for (solid circles) and against (solid squares) each species as a function of the starting global frequency. In all cases, patch-level selection substantially alters the cloud of variation, reducing the frequency of species that cause extinction and increasing the frequency of species that prevent extinction. In all cases, the new equilibrium frequencies are accompanied by a restructuring of the entire metacommunity (not shown in Fig. 11), altering the array of background communities experienced by species i .

Spot analysis of ten metacommunities (M11–M19). — To see if the other metacommunities governed by three-dimensional matrices are as conducive to patch-level selection as M13, two species, chosen at random from each of the other nine metacommunities, were subjected to the procedure outlined above. The open circles and squares in Fig. 11 show that the global frequency of most species can be altered by patch-level selection. Two conspicuous exceptions are species 1 and 9 from matrix M19, whose frequencies are unaltered by patch-level extinction (i.e., they lie on the 45° line that represents the initial global frequency). This is expected, since M19 is the only metacommunity governed by three-dimensional matrices that does not maintain a cloud of variation (see *Three-dimensional interaction matrices: The interaction matrix*, above).

To summarize, when certain regions of the “cloud of variation” contribute differentially to the dispersal pool, the entire cloud can change its shape to become concentrated in those regions.

DISCUSSION

As previously mentioned, any single study of complex interactions in metacommunities can explore only a tiny fraction of the parameter space. With respect to complex interactions, this study does not even include predator–prey and mutualistic relationships. With respect to metacommunities, this study is confined to the subdivided-population model and doesn’t include the island and stepping-stone models, in which dispersal occurs between patches that persist indefinitely. In this study environmental heterogeneity is absent and stochastic events occur only during the colonization of patches, after which everything is deterministic. Another limitation involves the level of analysis. Ideally we would like to understand the dynamics of single metacommunities in great detail. Although this is possible for selected cases (e.g., *Results: Two-dimensional interaction matrices: The interaction matrix* and *Numbers of colonizing individuals . . .*, above), the very fact that we are trying to model *complexity* necessitates a different kind of analysis, in which the effects of parameter values (such as rate of increase) on aggregate properties (such as global species diversity and variance among patches) are monitored for a sample of metacommunities. Two levels of analysis are required for empirical studies of biological communities in addition to simulation studies, and are often what the terms “reductionism” and “holism” are intended to mean (Wilson 1988).

Despite its limitations, this study provides a number of insights into the joint effects of complex interactions and spatial subdivision on the dynamics of biological communities. The first insight is that spatial subdivision can have no effect at all. In numerous simulation runs the global proportions of species became “centered” over a single domain of attraction, despite the fact that multiple domains existed for the entire dy-

namical landscape. The "cloud" of variation created by sampling error fell almost entirely within the single domain, whereupon the effect of deterministic interactions was to eliminate variation among patches. This result has implications for empirical studies of complex interactions. For example, Drake (1991, 1992) and Robinson and Edgemon (1988) have shown that the trajectories of aquatic microcosm communities depend on initial conditions, in particular on the sequence in which the species are introduced. However, their studies are analogous to the first cycle of the simulation runs reported here, in which the relative proportions of species in the dispersal pool are arbitrarily defined. It would be interesting to continue these experiments over several cycles, in which the microcosms become the dispersal pool for another set of microcosms, to see if diversity is maintained at global equilibrium or if the metacommunity collapses to a much smaller number of species.

Another interesting and counter-intuitive result is that species might fail to coexist in a metacommunity despite the fact that they coexist in a stable equilibrium in all mixed patches (see *Results: Two-dimensional interaction matrices: Numbers of colonizing individuals* . . . , above). This provides a counterexample to the more common expectation that locally unstable interactions can be stabilized by population structure (e.g., Levin 1974, 1976, 1978, Whittaker and Levin 1977, Hastings 1988, Taylor 1990, Hanksi and Gilpin 1991, Hassel et al. 1991).

Perhaps the most important result concerns the effects of complex interactions on global species diversity. In this study, sensitivity to initial conditions was increased in two ways—(a) by increasing the response term of the logistic equation (R), and (b) by changing the interaction coefficients from constants (the two-dimensional matrices) to linear functions of local community composition (the three-dimensional matrices). In both cases, global species diversity tended to increase, sometimes dramatically. If increasing sensitivity to initial conditions is envisioned as shrinking the domains of attraction on the dynamical landscape (or, alternatively, as increasing the momentum of points as they move over the landscape), at some point the cloud of variation created by sampling error will no longer "fit" into a single basin. Deterministic interactions will then expand the cloud of variation, which by definition means that different species will be favored in different patches (Segel and Jackson 1972, Levin and Segel 1976, and Levin 1979 examine a similar process for continuously distributed populations). Sensitive dependence therefore creates a form of heterogeneity even when none exists in the physical environment. Viewing metacommunities as clouds of variation placed on a complex dynamical landscape makes the idea of endogenously created heterogeneity appear quite reasonable. Perhaps additional simulations will show that it follows from sensitive depen-

dence in general, rather than from the specific assumptions of this model.

IMPLICATIONS FOR NATURAL SELECTION AT THE PATCH LEVEL

The idea that biological communities should somehow function well as whole systems has a long history in community and ecosystem ecology. Sometimes it is stated axiomatically, without any attention to the mechanisms that might produce functional organization (e.g., Clements and Shelford 1939, Emerson 1960, Odum 1969, Lovelock 1979). Sometimes it is not explicitly stated at all, but nevertheless appears as an intuition that communities should evolve to be productive, efficient, stable, diverse, persistent, or rich in "information" (e.g., Margalef 1968).

Careful attempts to model the evolution of functionally organized communities encounter a fundamental problem: Adaptation at any level requires a process of natural selection operating *at that level* (Dunbar 1960, 1972, Williams 1966, Lewontin 1970, May 1978, Slatkin and Wilson 1979, Wilson and Sober 1989). Furthermore, traits that are adaptive at lower levels (such as the individual) can easily disrupt function at higher levels (such as the community). For example, a virulent endosymbiont may well increase its relative frequency within single hosts, but may also increase the probability that the host—and the entire community of endosymbionts within the host—will die (see Wilson [1976, 1980, 1983a, b, 1986] and Wilson and Knollenberg [1987] for other examples). A community of well-adapted individuals is not the same as a well-adapted community.

Natural selection at the community level therefore requires a number of conditions: (a) a *population* of local communities (i.e., a metacommunity), that (b) *varies* in their species and/or genetic composition, and (c) corresponding variation in the productivity and/or extinction of local communities. For example, if the virulent endosymbiont is more common in some hosts than others, with corresponding variation in host mortality, less virulent or even mutualistic endosymbionts may prevail despite the fact that they are competitively inferior to the virulent type within hosts.

Most treatments of this problem make two critical assumptions—(a) that variation between patches is caused by sampling error, and therefore declines with the number of individuals colonizing the patches, and (b) that a conflict exists between levels of selection, so that interactions within patches favor species that disrupt community-level function. Viewing metacommunities as dynamical clouds of variation may allow both of these assumptions to be partially relaxed. First, complex interactions expand the cloud of variation that is required for any natural selection process to act. Second, they provide a spectrum of background communities that can either favor or inhibit any particular species. Within-patch selection is not an externally de-

finer parameter but can itself be shaped by between-patch selection. As a result, species that harm (or benefit) the whole system can also be suppressed (or promoted) within the system, reducing or even eliminating conflicts between levels of selection (Boyd and Richerson [1990] explore a similar process for individuals in social groups). Complex interactions in metacommunities might therefore enhance the evolutionary mechanisms required for local communities to function well as whole systems.

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