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COMMUNITY-ASSEMBLY MECHANICS AND THE STRUCTURE OF AN EXPERIMENTAL SPECIES ENSEMBLE

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Abstract.—It was relatively easy to produce alternative community states as a function of variability in a sequence of species invasions employed to assemble a community. Numerous mechanisms and processes are capable of producing both temporary and nonrecoverable differences in community structure. They include priority effects, intransitivities, emergent properties (e.g., vulnerability to invasion, specific topologies), and effects specific to differences in assembly sequences themselves. In ecological systems, the existence of alternative states presents a difficult comparative problem in the search for unifying principles that might underlie community-level organization. This problem can be solved only if we understand the cause of alternative states and determine whether such states are persistent or transient. Otherwise, ecological communities appear so variable that general principles and mechanisms elude detection, even if they exert a powerful influence over the structure of the system. Mechanisms that are documented as controlling community organization and the population dynamics of component species are not necessarily the mechanisms responsible for observed patterns. Factors uncovered in any extant community may be responsible only for maintaining the status quo. The reason these factors (e.g., competition, predation, parasitism) are currently operating is often a direct function of community-assembly mechanics. Community-assembly processes and dynamics must be understood if we are to discern properly between maintenance and causal mechanisms.

Interactions among species and the resulting community patterns have often been implicated as mechanisms that influence ecological communities (see, e.g., Cody and Diamond 1975; Connell and Slatyer 1977; Tilman 1977, 1982; Cohen 1978; Paine 1980; Pimm 1982; Schoener 1983; Sugihara 1983, 1985; Strong et al. 1984; Sih et al. 1985; Diamond and Case 1986; Thorpe 1986; Gray et al. 1987). The identification of such mechanisms and the patterns they generate has been an explicit goal of community-ecology research. Although the effects of some mechanisms (e.g., competition and predation) are well understood in some ecological systems, the action of these mechanisms across disparate community types (e.g., intertidal, freshwater, temperate-forest, and grassland systems), and even among similar community types, is far from consistent. Patterns may differ from one system to another even though the species composition may be similar and the same interspecific interactions or other mechanisms function in both. For example, in some ecological systems, consumers are able to ameliorate an unstable competitive interaction between prey species (Paine 1966). Although this phe-

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nomenon occurs in some rocky-intertidal benthic systems (two-dimensional systems, in the sense of Briand and Cohen 1987), it has not been found in analogous freshwater benthic systems (also two-dimensional systems; Thorpe and Berge 1981; Thorpe 1986). At this level, the search for generality in community ecology has been thwarted by such seemingly irreconcilable variability.

In addition to differences observed across community types, substantial differences often exist between communities that draw on essentially the same regional species pool (Sutherland 1974; Diamond 1975; Sale and Williams 1982; Sale 1984; Abrams et al. 1985; McCune and Allen 1985; Wilbur and Alford 1985; Gilpin et al. 1986). In many cases, differences between such communities represent alternative states (cf. Sutherland 1974; Connell and Sousa 1983). Several studies have shown that the existence of such states can be due to differences in how the communities were assembled (Gilpin and Case 1976; Sugihara 1982, 1983, 1985; Cole 1983; Drake 1983, 1985, 1988, 1990; Gilpin et al. 1986; Robinson and Dickerson 1987; Barkai and McQuaid 1988; Robinson and Edgemon 1988). A number of these studies have implicated the sequence of species invasions as the primary determinant of community organization (Cole 1983; Drake 1985; Wilbur and Alford 1985; Gilpin et al. 1986; Robinson and Dickerson 1987). Whether such states are persistent or are simply transient clearly depends on scale, and the implications of scale have only recently been explored (Allen and Starr 1982; Connell and Sousa 1983; Davis 1986; O'Neill et al. 1986).

I believe that the difficulty in understanding community-level properties and processes has two basic causes. First, it is clear that the vast majority of "community" studies actually investigate something other than communities. Most often guilds and taxonomically defined associations are considered communities, although they possess only some of the properties attributed to ecological communities (see discussions in Hutchinson 1978; Pimm 1982; Yodzis 1982; Schoener 1986; Cohen and Newman 1988; Paine 1988; Pimm and Kitching 1988). The ramifications of inconsistent usage are enormous (Drake 1990). For example, numerous studies have shown that widely disparate taxa often interact directly, and cascading or indirect effects can be shown in many systems (Kodric-Brown and Brown 1979; Brown et al. 1981; Carpenter et al. 1985; Kneib 1988). Accordingly, analysis of community components alone is of limited value.

Should one conclude, for example, that nonequilibrium dynamics characterize a community because a small species set—say, a guild of birds, lizards, or insects—varies through time, even though it may represent a minute fraction of the species and biomass contained in the community? The answer to this question is a resounding no. Ecological communities are ensembles of species delimited by the practical extent of species connectivity. Connectivity is defined in terms of energy flow, nutrient dynamics, and any mechanism whereby the population dynamics of one species are influenced by another. This definition clearly spans all trophic levels and includes species and processes operating at divergent scale levels (Allen and Starr 1982; O'Neill et al. 1986). Critics of this definition plead unwieldy complexity, but I believe it is essential to direct community-level questions at communities and not at community components. Analysis of components

alone offers a glimpse of community processes, but even experimental manipulations of such components may fail to uncover the correct mechanisms.

The second and perhaps more serious source of difficulty is the conceptual framework in which most communities are studied and analyzed. Because most community-level studies are of relatively short time frames (normally a few years and spanning a few generations), it is difficult to uncover organizational factors when the subject system may have a complex history. Communities are historically derived structures because past events often influence the current state. Therefore, we must ask, when can historical effects be cast aside, and when are they critical to system organization? Clearly, if we consider only alternative community states, while ignoring the trajectories that produced those states, communities may well "appear" highly idiosyncratic upon comparison when indeed they are not. Such variation can be mechanistically driven while being indistinguishable from a random expectation. We may expect the communities to have similar species composition, trophic structure, and other properties, but the properties may be very different without our understanding why. As a result, generalization between and within ecological systems has proved difficult, if not impossible, at all but the most simple levels. I suggest that the mechanisms responsible for pattern uncovered in most community studies may simply be the mechanisms maintaining currently observed patterns. The more fundamental organizational factors (e.g., the mechanisms ultimately responsible for community structure) may be hidden in the mechanics of community assembly (Drake 1985, 1988, 1990; Ricklefs 1987; Crawley 1989).

The consequences of the historical nature of communities are considerable. What can one conclude if a study identifies the mechanisms responsible for the maintenance of structure at some period of time? Simply put, the conclusion is that these mechanisms have been identified and that they are capable of maintaining the pattern at hand. I must stress, however, that such a study has not necessarily identified the factors ultimately responsible for producing the observed patterns (Thorpe 1986). Thus, I believe that maintenance and causality are often independent of each other. In a number of studies supporting this view, events that occur during community development, succession, or assembly can lead to differences in community structure (Sutherland 1974; Cole 1983; Sale 1984; Abrams et al. 1985; Alford and Wilbur 1985; Drake 1985, 1988; Wilbur and Alford 1985; Gilpin et al. 1986; Gaines and Roughgarden 1987; Robinson and Dickerson 1987; Crawley 1989; see also Horn 1976; McCune and Allen 1985; Mortimer 1987; and caution in Connell and Sousa 1983). Often events or assembly steps cannot be seen in hindsight; yet the events may have permanently affected community structure. In such cases, the mechanisms that operate after the systems diverge are only partially responsible for observed patterns. The event that initiated divergence may determine which mechanisms are subsequently possible, particularly if that factor alters community membership. Because different assembly trajectories may produce different community states, it is not clear whether an examination of extant ecological systems alone can reveal which mechanisms are responsible for producing observed pattern. An understanding of the mechan-

ics of community assembly may well be the first step toward development of a general theory of organization at the community level (Drake 1990; DeAngelis and Teramoto, in press).

In this study, I examine the role that historical factors and assembly mechanics play in producing pattern in a freshwater laboratory ecosystem. These microecosystems provide a highly controlled experimental system with which to investigate community-level phenomena. They represent simple models of community processes and are thus an abstraction of natural communities. However, the use of such models is arguably the only method currently available for addressing the points mentioned above. The experimental protocol was to introduce species (ranging from bacteria through invertebrate predators) in sequence and thereby to subject an initially sterile environment to invasion, resulting in communities with known assembly histories. I asked the following questions: How does the sequence of species invasions, the equivalent of historical variation in community assembly, influence community structure? How does timing between invasions influence community structure? Can alternative community states (in terms of the relative abundance and composition of species) be produced simply as a function of assembly history? Is it possible to determine rules that govern community assembly and generate subsequent patterns? And can these rules be used to produce communities with specific properties? Questions such as these strike near the heart of community ecology; yet the answers are largely unknown.

EXPERIMENTAL DESIGN AND METHODS

To explore the effect of history and assembly dynamics on community organization, I constructed experimental communities under controlled laboratory conditions using different sequences of species invasion. Simply, I defined a set of species and then permuted the sequence of invasions, allowing each community to be colonized by all species in the species pool. Although artificial, a laboratory system was essential because of the need for complete control over species composition as the communities were assembled. There are clear assumptions built into my choice of experimental system and set of species. This is not an issue, however, because I was interested in the phenomenon of community assembly. Exploring phenomenology under controlled conditions seemed an appropriate first step toward exploring that phenomenon in nature.

In this study, I used two types of microecosystems. The first type of microecosystem (small systems) held a volume of 0.25 L (250-mL flasks). The second type of microecosystem (large systems) held 40 L (40-L glass aquaria). The large systems were used to explore the dynamics of community assembly using 10 different assembly routes or temporal sequences of invasion. The small systems were used to explore competitive interactions and sequence effects among species found to be key components of the large systems. These two systems also allowed me to examine the roles of spatial scale and absolute population abundance during community assembly. In addition to volume, I varied the period of time (10 vs. 15 d) between introductions in selected small and large systems. The large systems also differed from the small systems in that consumers were allowed to

TABLE 1

SPECIES USED IN THE SMALL AND LARGE MICROECOSYSTEM STUDIES

Type	Species
Producers	*Ankistrodesmus falcatus* var. *acularis**
	*Scenedesmus quadricauda**
	Chlamydomonas reinhardtii
	*Selenastrum bibrium**
Herbivores/ Predators	*Cypris* sp.* (Ostracoda)
	*Gammarus lacustris** (Amphipoda)
	*Daphnia magna** (Cladocera)
	Daphnia pulex (Cladocera)
	Simocephalus vetulus (Cladocera)
	Cyclops vernalis (Copepoda)
	Pleuroxus truncatus (Cladocera)
Protozoans	*Euglena gracilis*
	Paramecium multimicronucleatum
Bacteria	*Nitrosomonas* spp.
	Nitrobacter spp.

*The only species used in the small systems; all species were used in the large systems.

colonize before all producers had colonized. Furthermore, producer species colonized over a longer period of time than was allowed in the small-system experiments. In some treatments, the final producer colonist was introduced during day 45 of the experiment; in other treatments, 165 d elapsed before all producers had colonized.

I developed a synthetic freshwater medium capable of supporting both autotrophic and heterotrophic populations for extended periods of time, often exceeding 1 yr. This medium is a hybrid of the WC algal medium, a zooplankton medium (M. Lynch, personal communication), and the Woods Hole MBL medium. All experiments described here were conducted under static rather than continuous-flow conditions. Algal cultures were maintained on WC, MBL, or WC + P + C medium (Stein 1975). Invertebrates were cultured using a simple zooplankton medium supplemented with nitrifying bacteria (*Nitrosomonas* and *Nitrobacter*) and a vitamin mixture (M. Lynch, personal communication). I obtained axenic cultures of algae (*Ankistrodesmus falcatus, Selenastrum bibrium, Scenedesmus quadricauda,* and *Chlamydomonas reinhardtii*) from the Culture Collection of Algae at the University of Texas at Austin. Algae were cultured and maintained under axenic conditions throughout the experiment. The choice of species, including both producers and consumers, was based on availability and the relative ease of culture (table 1). These are generally common species and can be found coexisting in natural lakes and ponds.

Consumer species were obtained from natural ponds and lakes in north-central Indiana or from cultures with a known history. These species were cultured and maintained in the laboratory until needed. Although axenic cultures of algae and bacteria were relatively easy to maintain, pure cultures of consumers were not. Consumer species simply cannot be maintained under axenic culture, because many of them require a bacterial fauna for metabolism or for a food source.

Similarly, some consumer species cannot be maintained for long on an artificial diet (e.g., yeast or cerophyll and accompanying bacterial fauna) (personal observation; Goulden et al. 1982). Hence, no attempt was made to maintain axenic consumer cultures.

To avoid possible contamination when consumers were introduced to a microecosystem, I developed a simple rinsing procedure. This procedure significantly reduced the chance of inadvertent contamination. Rinsing consisted of the following series of rinses: (1) a sterile-medium rinse; (2) a sterile-medium rinse containing a broad-spectrum herbicide; (3) a sterile-medium rinse containing a broad-spectrum antibiotic; and (4) a final rinse in sterile medium. During each rinsing stage, the organisms soaked for 1 h. Although some mortality was associated with this procedure for some species, the mortality rate never exceeded 20% of the treated population. Fecundity was not reduced among surviving individuals. Using this procedure, I was able to eliminate algal contamination from all but two of the 40 large microecosystems. No contaminants were found in the small systems. I found it impossible to control bacterial colonization.

All microecosystems were housed in an environmentally controlled room at 20°C. A 12L:12D photoperiod was established using white-light fluorescent bulbs that produced 2,000 lux at the microecosystem surface. To reduce evaporation and potential airborne contamination, the large microecosystems were fitted with glass covers and the small microecosystems were sealed with Parafilm. Laboratory air was washed, electrostatically filtered, and periodically flooded with germicidal ultraviolet light. I used sterile technique whenever microecosystems or cultures were handled.

For the microecosystems described above, communities were assembled by adding species in a predetermined sequence to each microecosystem. Varying species introduction or invasion sequences and varying the period of time between successive introductions were the primary experimental treatments (tables 2, 3). Sequence-control treatments were also established during which all species were introduced simultaneously. Other factors that varied between the small and large systems included volume and associated environmental variables such as depth, distribution of light, and the ratio of surface area to volume. Initially, species were introduced into the small microecosystems every 10 d and into the large microecosystems every 15 d. The length of time between introductions in the small and large systems was later reversed in selected treatments. This allowed me to explore any effects resulting from volume and variances in timing between successive invasions. Each of the large-system treatments was performed four times, and treatments were performed three times in the small systems. I introduced producers to the microecosystems by adding cells, resulting in an inoculation density of 10^4 cells mL^{-1}. Producers were always obtained from cultures exhibiting log-phase growth, although precise culture age was not controlled. This reduced potential variations in the physiological condition of algal populations upon introduction.

Consumers were introduced to the microecosystems using an arbitrary population size of 15 individuals. Among consumers that reproduce sexually and for which sex was easily determinable (e.g., Copepoda, Amphipoda), 10 females and

TABLE 2

SEQUENCES OF SPECIES INVASION IN THE LARGE MICROECOSYSTEMS

	PERIOD OF INTRODUCTION*												
TREATMENT	1	2	3	4	5	6	7	8	9	10	11	12	13
1	AK	SI	SE	CP	CH	EU	GA	PA	MA	CY	PL	SC	PU
2	SC	SE	CH	AK	PL	PA	MA	SI	CY	PU	EU	CP	GA
3	SE	MA	PL	CH	AK	CP	SC	EU	PU	PA	GA	SI	CY
4	CH	AK	SC	SI	MA	GA	SE	CP	PU	EU	PL	PA	CY
5	SC	CH	CP	SI	PA	AK	EU	CY	SE	GA	MA	PL	PU
6	SE	CH	PU	EU	SC	PL	CP	SI	MA	AK	PA	CY	GA
7	AK	CP	SI	MA	PL	SC	PA	CH	GA	SE	EU	PU	CY
8	CH	MA	AK	PL	SE	EU	SC	CP	PU	PA	SI	CY	GA
9	SC	AK	CH	SE	EU	PA	CP	MA	CY	PU	PL	GA	SI
10	AK	SE	CH	SC	GA	MA	PA	PL	PU	CP	EU	CY	SI
Control	All species												

NOTE.—AK, *Ankistrodesmus falcatus;* SC, *Scenedesmus quadricauda;* SE, *Selenastrum bibrium;* CH, *Chlamydomonas reinhardtii;* MA, *Daphnia magna;* PU, *Daphnia pulex;* SI, *Simocephalus vetulus;* CP, *Cypris* sp.; GA, *Gammarus lacustris;* CY, *Cyclops vernalis;* EU, *Euglena gracilis;* PA, *Paramecium multimicronucleatum;* PL, *Pleuroxus truncatus.* Each treatment was inoculated with the nitrifying bacteria *Nitrosomonas* and *Nitrobacter* along with the first species introduction. In each treatment, the first species introduced was always a primary producer. After the first producer introduction, consumers as well as other producers were eligible for colonization. In the sequence control treatment, all species were introduced at the same time. Each treatment was replicated four times.

*Species were introduced at 15-d intervals; 1 is day zero, 2 is day 15, etc.

TABLE 3

SEQUENCES OF SPECIES INVASION IN THE SMALL MICROECOSYSTEMS

	PERIOD OF INTRODUCTION*			
TREATMENT	1	2	3	4
1	SC	AK	SE	Consumers
2	SC	SE	AK	Consumers
3	SE	AK	SC	Consumers
4	SE	SC	AK	Consumers
5	AK	SE	SC	Consumers
6	AK	SC	SE	Consumers
Control	All species			

NOTE.—SC, *Scenedesmus quadricauda;* SE, *Selenastrum bibrium;* AK, *Ankistrodesmus falcatus;* consumers (*Gammarus lacustris, Cypris* sp., *Daphnia magna*). A 10-d period was allowed between species introductions. At day 80, the three consumer species were introduced simultaneously. In the sequence control treatment, all species colonized at the same time. Each treatment was performed three times.

*Species were introduced at 15-d intervals; 1 is day zero; 2 is day 15, etc.

5 males were introduced. In some species, it was also possible to standardize reproductive state. For example, only female copepods that possessed egg sacs were introduced. For some species, it was impossible to standardize reproductive condition and sex (e.g., Ostracoda). In such cases, a random sample of individuals was introduced. Among asexual species with observable propagules, the reproductive state (e.g., presence of embryos in Cladocera) was standardized. If a consumer species became extinct or suffered substantial mortality within the initial 24-h period after it was introduced, it was reintroduced once again using the protocol described above. This reduced the probability of extinction caused by chance factors.

Producers were censused by withdrawing 1-mL subsamples and directly counting individuals in a Sedgwick-Rafter cell. Before censusing, each system was gently homogenized by stirring, and any surface film that developed on the microecosystem walls was resuspended. Water samples were taken by withdrawing a volume of 1 mL by pipette. A stratified random procedure was used to avoid bias in sampling. In this procedure, water was sampled from surface, bottom, mid-water, and side sections of the large systems. Stratification was not required in the small systems because of size. The Sedgwick-Rafter cell was also stratified into five sections, and randomly chosen fields of view were counted within each section. Sampling was conducted without replacement to avoid potential contamination. This procedure was thoroughly tested and yielded estimates of the population mean with an error of less than 5% (ANOVA) at the population levels encountered throughout most of the study. When a producer was not found, I scanned the length of the sampling chamber several times and noted presence or absence.

Consumers were censused by directly counting individuals in situ. Attempts were made to sample consumer abundance by withdrawing replicate volumes of water for direct observation (see, e.g., Neill 1975). However, during this study I found this protocol too invasive because of the high probability of inadvertent contamination. Occasionally, a consumer species became highly abundant, making accurate whole counts difficult. In such cases, abundance was estimated by repeated visual counts. Species that became rare were noted as present or absent after the microecosystems were thoroughly searched. I found only one case in which a consumer species that apparently had become extinct reappeared in a subsequent census.

RESULTS

Assembly Mechanics: Small Systems

Producer assembly.—The population growth characteristics of each producer species (*Scenedesmus quadricauda, Selenastrum bibrium,* and *Ankistrodesmus falcatus*), growing in the absence of interspecific interference, were established using replicated single-species control treatments (table 4). *Chlamydomonas reinhardtii* was not used in the small systems. Both *Selenastrum* and *Ankistrodesmus* produced significantly larger populations than did *Scenedesmus* during all stages

TABLE 4

MEAN PER CAPITA DAILY GROWTH RATE OF *SCENEDESMUS QUADRICAUDA* (SC), *ANKISTRODESMUS FALCATUS* (AK), AND *SELENASTRUM BIBRIUM* (SE) DURING THE FIRST TEN-DAY PERIOD AFTER INTRODUCTION IN THE SMALL SYSTEMS

ASSEMBLY SEQUENCE	SPECIES		
	SC	SE	AK
	$\bar{X}$ (SD)	$\bar{X}$ (SD)	$\bar{X}$ (SD)
SC-AK-SE	.17 (.01)	.03 (.01)	−.09 (.01)
SC-SE-AK	.17 (.02)	.01 (<.01)	−.01 (<.00)
AK-SC-SE	.18 (<.00)	.03 (<.00)	.18 (.04)
AK-SE-SC	.23 (.02)	.07 (<.00)	.19 (.02)
SE-SC-AK	.21 (<.00)	.24 (.03)	.06 (.01)
SE-AK-SC	.22 (.02)	.23 (.04)	.05 (.01)
Nonsequenced	.16 (.02)	.09 (.04)	.05 (.01)
Single-species controls	.20 (.01)	.27 (.01)	.22 (.07)

NOTE.—Mean daily growth rates and standard deviation are calculated from three replicates of each assembly sequence. The growth rate of *Scenedesmus quadricauda* increased considerably in all treatments during the second, and nearly all subsequent, 10-d intercensus periods (see fig. 1). Both *Selenastrum bibrium* and *Ankistrodesmus falcatus* showed occasional minor increases in growth rate. Furthermore, as *S. quadricauda* increased, the growth rate of *S. bibrium* and *A. falcatus* fell to zero or became negative.

of interspecific free population growth. After 60 d of growth, both *Ankistrodesmus* and *Selenastrum* produced populations exceeding 2×10^6 cells mL^{-1}, whereas *Scenedesmus* never reached 10^6 cells mL^{-1}. The abundance of *Selenastrum* was significantly larger than that of *Ankistrodesmus* (Student's $t = 4.24$, $P < .05$), and both of these species' abundances were significantly larger than that of *Scenedesmus* ($t = 7.33$, $P < .05$; $t = 24.82$, $P < .05$, respectively).

Despite the ability of both *Selenastrum* and *Ankistrodesmus* to outproduce *Scenedesmus* numerically in single-species controls, *Scenedesmus* became numerically dominant in all assembly treatments (fig. 1). The abundance of both *Selenastrum* and *Ankistrodesmus* was always severely depressed in these treatments. This result always occurred, regardless of when *Scenedesmus* was introduced in the assembly sequence. Per capita daily growth rates were estimated for all species, assuming a simple exponential-growth model for the first 10 d of population growth following invasion (table 4). In contrast to the indifference of *Scenedesmus* to its time of introduction, the population growth rates of both *Ankistrodesmus* and *Selenastrum* were strongly influenced by the introduction order (table 4). Both species developed substantial populations when they were introduced first, reaching up to 3.2×10^5 cells mL^{-1} before *Scenedesmus* was introduced. However, this initial period of growth was always severely damped by the subsequent invasion and population growth of *Scenedesmus* (fig. 1*A,B, C,F*). When introduced after *Scenedesmus* in any invasion sequence, neither of these species was able to increase in abundance much above introduction levels. By any measure of interspecific competition, under the given conditions of the experiment, *Scenedesmus* is clearly the superior competitor.

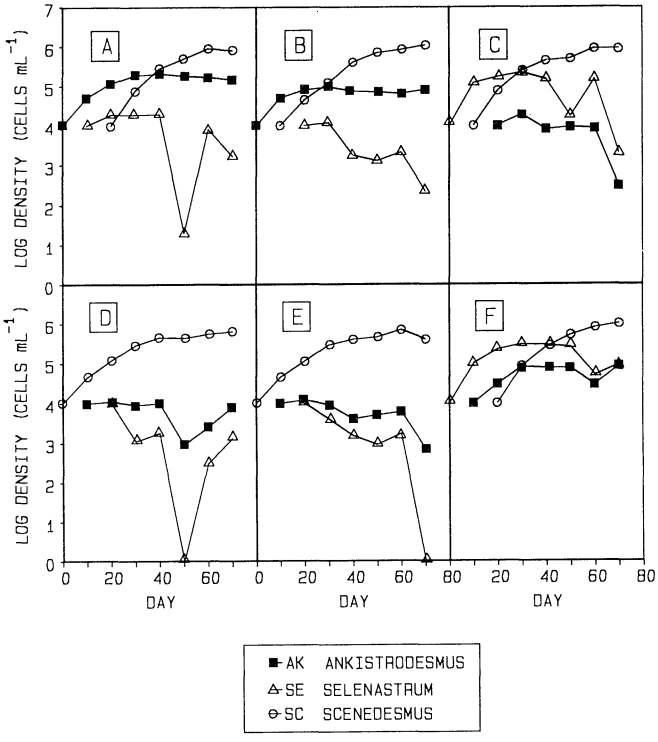


FIG. 1.—Population-growth trajectories of producers during the small-system assembly experiment. Species: AK, *Ankistrodesmus falcatus;* SE, *Selenastrum bibrium;* SC, *Scenedesmus quadricauda.* Each panel represents a different sequence of species invasions. Sequence is identified by the order of species listed within each panel. Three replicates of each treatment were conducted. Mean values and the standard deviation about the mean are reported. *Scenedesmus* always became the dominant species in each treatment.

Although alterations to the invasion sequence had no effect on species' dominance relationships, some assembly sequences resulted in different patterns of species' relative abundances. For example, in assembly sequences in which *Scenedesmus* was the first invader, the other species became either extremely rare or extinct (fig. 1*D,E*). Long-term coexistence was possible only when *Scenedesmus* colonized at a later stage during the assembly sequence. However, even in these cases, species' relative abundance was strongly skewed toward *Scenedesmus.* During the sequence in which *Selenastrum* invaded first, followed by *Scenedesmus* and *Ankistrodesmus,* all but *Scenedesmus* eventually became extinct (fig. 1*C*). However, when *Ankistrodesmus* colonized first, followed by *Selenastrum* and *Scenedesmus,* all three species coexisted over the term of the experiment (fig. 1*A*).

How did the populations behave in systems in which all three species colonized simultaneously? *Scenedesmus* again became the dominant species, and populations of the other algae increased hardly above introduction levels. In this treat-

ment, all species but *Scenedesmus* became extinct. The effect of *Scenedesmus* on the abundance of the other producers was strong in all assembly trajectories. Nevertheless, two alternative community states developed as a function of assembly sequence: communities containing only *Scenedesmus,* and communities dominated by *Scenedesmus* but with small, persistent populations of the other two species. Differences in assembly sequence channeled each community to one of these two community states or attractors.

Consumer assembly.—After the producer species' relative dominance had been clearly established (day 80), I explored each community's vulnerability to invasion by an identical set of consumers. Because these systems were small in volume, I introduced only a subset of the consumer species that were introduced to the large systems. These species included *Daphnia magna* (Cladocera), *Cypris* sp. (Ostracoda), and *Gammarus lacustris* (Amphipoda). In preliminary studies and in the large-system assembly experiments, these species tended to be among the most successful invaders. I found no difference among treatments regarding invasion vulnerability by these species. All three species successfully colonized and persisted over 30 d in all treatments. However, only *D. magna* and *Cypris* species were able to reproduce in these treatments during that period of time. The population abundance of producers decreased after consumer invasion; however, there was no change in dominance. By day 130, 50 d after consumer invasion, all consumer species had become extinct in all treatments. During this period of time, producer populations showed signs of becoming senescent, and the small-system experiment was terminated.

Assembly Dynamics: Large Systems

Primary producers.—The order of species' introduction significantly affected invasion success and ultimately relative abundance in the large systems, although it did not in the small systems. The effect of invasion sequence on assembly dynamics was so strong that order was the primary determinant of a producer's relative abundance. In 40% of all treatment replicates (16 of 40 replicates), the dominant producer species ($P < .05$) at the termination of the experiment was the first producer to invade (table 5). In half the treatments (1, 4, 5, 7, 10), the dominant species was the same in all replicates. For example, in treatment 5, *Scenedesmus* was the most abundant producer in all replicates. Each of the remaining three species was second in numerical abundance in one or more of the remaining replicates. The remaining treatments (2, 3, 6, 8, 9) had some variation in the dominant producer species. In treatments 2, 3, and 6, only a single replicate deviated. The overall proportional length of time over which the initial producer colonist remained dominant during the course of community assembly varied from 0.15 (*Ankistrodesmus,* treatment 10) to 1.00 (*Ankistrodesmus,* treatment 7).

In two treatments (4, 10), the initial producer colonist was unable to maintain numerical dominance in any of the replicates. Here, the initial colonist was rapidly overtaken by the next producer to invade. In one case, *Chlamydomonas* colonized first and was then rapidly replaced by *Ankistrodesmus*. In the other case, *Ankistrodesmus* colonized first and was replaced by *Selenastrum*. The two treatments in which *Ankistrodesmus* colonized first illustrate the dramatic effect

TABLE 5

RELATIVE DOMINANCE OF PRIMARY PRODUCERS IN THE LARGE SYSTEMS AFTER COMPLETION OF THE ASSEMBLY SEQUENCES, DAY 195 OF THE EXPERIMENT

Treatment/ Replicate	Sequence of Producer Invasions	Order of Relative Dominance				Proximity Invasions (days)	Proportion of Time Dominant
1-1	AK-SE-CH-SC	AK	CH	SE	SC*	120	.98
1-2		AK	CH	SE*	SC*		
1-3		*AK*	*CH*	SE	SC*		
1-4		AK	CH	SE	SC*		
2-1	SC-SE-CH-AK	SC	CH	*SE*	*AK*	60	.94
2-2		SC	CH	*SE*	*AK*		
2-3		SC	CH	*SE*	*AK*		
2-4		*AK*	*SC*	*SE*	*CH*		
3-1	SE-CH-AK-SC	SE	AK	SC	CH*	105	.95
3-2		...	...	...	...		
3-3		SE	AK	*SC*	*CH*		
3-4		*AK*	*SE*	*SC*	*CH*		
4-1	CH-AK-SC-SE	*AK*	*CH*	*SE*	*SC*	105	.29
4-2		AK	SC	*SE*	*CH*		
4-3		AK	SC	SE	CH		
4-4		AK	SE	SC	CH		
5-1	SC-CH-AK-SE	SC	*AK*	*CH*	*SE*	135	.88
5-2		SC	*AK*	*CH*	*SE*		
5-3		SC	*AK*	*CH*	*SE*		
5-4		SC	*AK*	*CH*	*SE*		
6-1	SE-CH-SC-AK	SE	AK	SC	CH*	150	.98
6-2		SE	CH	SC	AK		
6-3		SE	AK	*SC*	*CH*		
6-4		AK	*SC*	*SE*	CH*		
7-1	AK-SC-CH-SE	AK	*CH*	*SC*	*SE*	150	1.00
7-2		AK	*CH*	*SC*	*SE*		
7-3		AK	CH	SC	SE*		
7-4		AK	CH	SC	SE*		
8-1	CH-AK-SE-SC	AK	SE	SC*	CH*	105	.40
8-2		*AK*	*SC*	*CH*	SE*		
8-3		*CH*	*SC*	AN	SE*		
8-4		*SE*	*SC*	AK	CH*		
9-1	SC-AK-CH-SE	AK	SC	SE	CH	60	.71
9-2		*SC*	*AK*	*SE*	CH*		
9-3		*SC*	*AK*	*SE*	CH*		
9-4		AK	SC	*SE*	CH*		
10-1	AK-SE-CH-SC	SE	SC	AK	CH*	60	.15
10-2		SE	SC	AK	CH*		
10-3		SE	SC	AK	CH		
10-4		SE	SC	AK	CH		

NOTE.—AK, *Ankistrodesmus falcatus;* CH, *Chlamydomonas reinhardtii;* SC, *Scenedesmus quadricauda;* SE, *Selenastrum bibrium.* Population sizes between species that were statistically indistinguishable between replicates ($P < .05$) are italicized (e.g., *AK CH*). Species that became extinct are noted with an asterisk (e.g., CH*). The proximity of invasions shows the number of days between the first and last producer introduction. Proportion dominant reflects the proportion of time (in time periods) that the first producer colonist was significantly ($P < .05$) more abundant than any other species. Replicate 2 of treatment 3 was terminated because of contamination.

TABLE 6

INITIAL MEAN PER CAPITA DAILY GROWTH RATES FOR *ANKISTRODESMUS FALCATUS* (AK), *SELENASTRUM BIBRIUM* (SE), *CHLAMYDOMONAS REINHARDTII* (CH), AND *SCENEDESMUS QUADRICAUDA* (SC) DURING THE FORTY-LITER (LARGE SYSTEMS) ASSEMBLY EXPERIMENTS

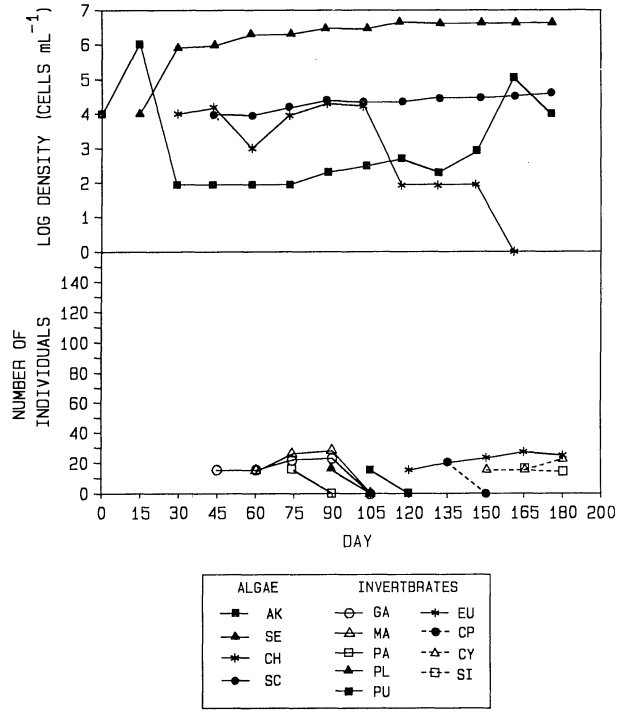
	Species			
	SC	SE	CH	AK
Sequence	$\bar{X}$ (SD)	$\bar{X}$ (SD)	$\bar{X}$ (SD)	$\bar{X}$ (SD)
AK-SE-CH-SC	Extinction	−.10 (.05)	−.09 (.17)	.16 (.01)
SC-SE-CH-AK	.09 (.01)	−.34 (.00)	.21 (.04)	−.12 (.04)
SE-CH-AK-SC	−.27 (.11)	.10 (.01)	.07 (.11)	−.01 (.02)
CH-AK-SC-SE	−.06 (.05)	−.17 (.11)	.36 (.01)	−.18 (.12)
SC-CH-AK-SE	.05 (.00)	−.26 (.11)	.06 (.17)	−.43 (.05)
SE-CH-SC-AK	−.12 (.02)	.22 (.01)	.11 (.03)	−.01 (.02)
AK-SC-CH-SE	−.23 (.15)	−.21 (.15)	−.17 (.07)	.17 (.01)
CH-AK-SE-SC	.13 (.08)	−.34 (.00)	.34 (.00)	−.10 (.16)
SC-AK-CH-SE	.04 (.01)	−.09 (.21)	−.10 (.21)	.00 (.73)
AK-SE-CH-SC	−.02 (.02)	.23 (.01)	−.63 (.19)	.34 (.00)

NOTE.—Producers were not introduced in sequence as in the small-system experiments; rather, a species could be introduced early (day 1) or as late as day 170 during the assembly sequence. Complete invasion sequences are listed in table 2. Each value is calculated from four replicates of each assembly sequence.

of invasion sequence and timing on community assembly. *Ankistrodesmus* quickly lost dominance when the system was invaded by *Selenastrum* during the next invasion event (treatment 10; table 5). However, in the other treatment (1)—when *Ankistrodesmus* invaded first—*Selenastrum* was also the second producer to invade. In this case, *Selenastrum* colonized 30 d after *Ankistrodesmus* rather than 15 d later as in the other treatment. Here, *Ankistrodesmus* maintained dominance. This effect was apparently due to the extended period of competition-free time that *Ankistrodesmus* experienced before invasion by *Selenastrum*. In the treatment in which *Ankistrodesmus* became dominant, the second colonist in the assembly sequence was a consumer (*Simocephalus vetulus*); however, this species did not successfully invade the system.

To explore the growth response of the initial species following invasion into different assembly sequences, I calculated mean per capita daily population growth rates for each of the species during the first 15 d after introduction (table 6). The population growth rates of both *Ankistrodesmus* and *Selenastrum,* when each species was the first invader, were similar to those seen in the small systems (table 4). The initial growth rate of *Scenedesmus,* on the other hand, was an order of magnitude lower in the large systems than in the small systems (Student's t, $P < .01$; tables 4, 6). This reduction in growth rate occurred even though the medium was identical and the invader's population density was the same. *Chlamydomonas* exhibited the fastest growth rate of any species when it invaded first, although in treatments in which it was not the first invader its initial growth rate was considerably lower. Despite the capability for rapid growth in *Chlamydomo-*

A.


LOG DENSITY (CELLS mL^{-1})
NUMBER OF INDIVIDUALS
DAY
ALGAE
AK
SE
CH
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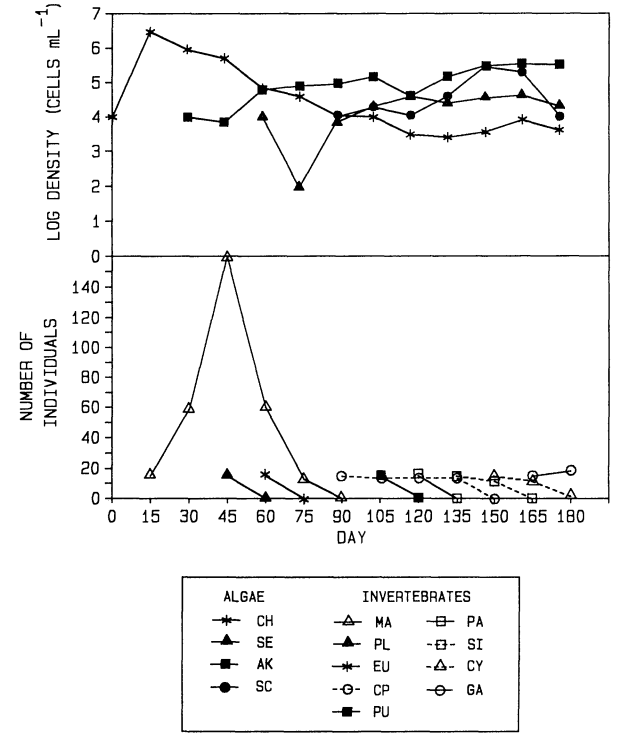
EU
CP
CY
SI

B.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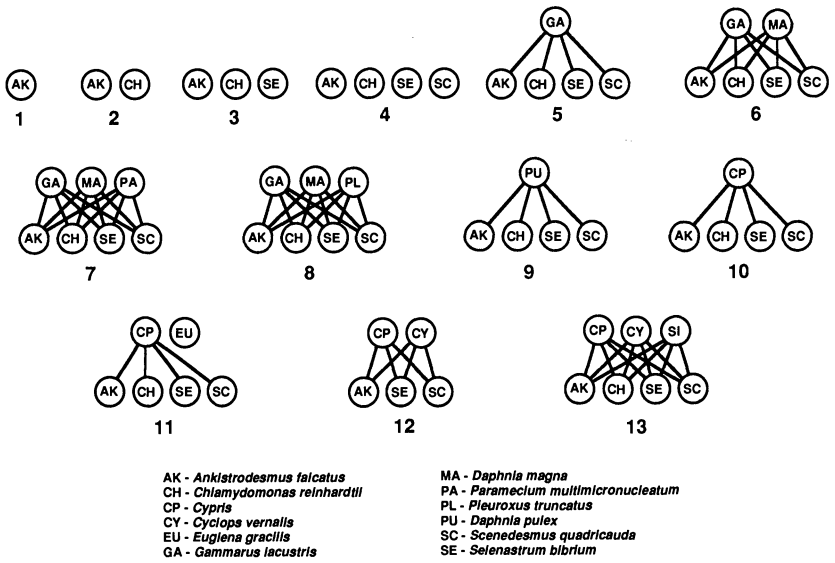
nas, this species was rarely able to maintain numerical dominance under any of the conditions explored here.

The overwhelming competitive advantage exhibited by *Scenedesmus* during all assembly sequences in the small systems was not seen in the large systems. Similarly, no other species exhibited the kind of dominance shown by *Scenedesmus* in the small systems. Representative population-growth trajectories seen among producer populations are illustrated in figure 2. A topological representation of two sets of trajectories is given in figure 3. Among assembly trajectories, considerable swings in population growth, ranging from simple boom and crash to sustained oscillations, were common. Although it was beyond the scope of this study to attribute cause to the fine-scale dynamic behavior of each population, some correlations between producer and consumer abundance were evident. Numerous controlled experiments would be required to understand the causal agents responsible for the observed population dynamics at each step during community assembly.

Consumer assembly.—Colonization and reproductive ability of consumers, as indexed by mean persistence time, varied considerably among the large-system treatments (table 7). Some treatments were readily invaded and supported large populations of several consumer species (figs. 2, 3). Other treatments proved difficult to colonize and were essentially resistant to invasion by all consumer species. In nearly all treatments, a consumer species either colonized and reproduced in an assembling community or became extinct before the next population census. In a few cases, some species were able to colonize a microecosystem treatment and persist for a brief period without reproducing.

Among consumers, *Daphnia magna, Cyclops vernalis, Cypris* sp., and *Gammarus lacustris* were the most successful invaders. These species successfully invaded at least half the treatments, and *D. magna* colonized all treatments. *Daphnia magna* functions as a filter-feeding herbivore. *Cypris* and *Gammarus* are also herbivores found foraging on the bottom or sides of the microecosystems. *Cypris* was often observed grazing on clumps of algae and feeding on the algal or bacterial film that developed on the dead invertebrates. *Cyclops vernalis* is normally a predator as an adult, but it clearly has the ability to capture and feed on small aggregations of algae. *Daphnia pulex* and *Simocephalus,* both herbivores, were short-term residents in some of the sequenced treatments; however, they were unsuccessful in most. *Simocephalus* was frequently found grazing on the microecosystem walls, whereas *D. pulex* was observed most often in the water column. *Pleuroxus truncatus* colonized in only a single treatment and per-

FIG. 2 (*facing page*).—Population-growth trajectories of both producers and consumers during community assembly in the large-system experiment: *A,* the results of assembly-treatment 10 (see table 2); *B,* the results of assembly-sequence 8. Producer population growth is depicted in the upper portion of each panel (reported as the number of cells per milliliter) and consumer population growth in the lower portion of each panel. Mean population abundances, plotted on a log scale, are calculated from four replicates of each treatment. Ten assembly sequences were explored during this study.



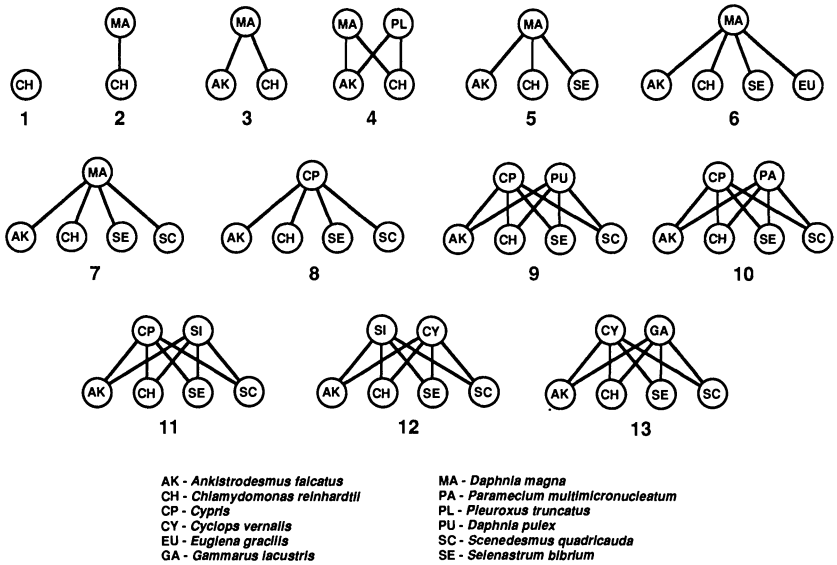


FIG. 3.—Topological, or food-web, representations of the assembly sequences illustrated in fig. 2. Species that became extinct during the course of assembly are removed from the food web. The two species of bacteria *Nitrosomonas* and *Nitrobacter* are not depicted in the food-web topologies, even though they persisted throughout the experiment. Maximum connectance among consumers and producers is assumed, although interaction strengths doubtless varied. The producer species used here were found in the guts of all consumer species. However, the degree to which specific consumer species were able to digest producers is not known for all species.

TABLE 7

MEAN PERSISTENCE TIME (DAYS) OF CONSUMER SPECIES USED IN THE LARGE SYSTEMS

	TREATMENT									
SPECIES	1	2	3	4	5	6	7	8	9	10
MA	30	23*	53	23	23	23	30	71	15*	38
CP	0	75	0	0	0	38	53	128	0	98
GA	0	23	38	0	0	23	0	68	0	53*
EU	0	0	0	0	0	0	0	0	0	0
PA	0	0	0	0	0	0	0	0	0	0
CY	23*	23	68	23	0	11*	23	15*	90	68
PL	0	0	0	0	0	0	0	23	0	0
PU	0	0	0	0	0	0	0	49*	0	0
SI	0	0	0	0	0	0	0	19	0	68
Total days	53	144	159	46	23	95	106	373	105	325

NOTE.—Microecosystems were censused at 15-d intervals. A species that persisted through one interval (15 d) but was extinct by the next is assigned an intermediate value. Hence, values of 23 (actually 22.5) represent species that persisted for one intersample interval but were extinct by the next interval. Values are rounded to the nearest whole day. In 23 of the 33 cases reported, there was no variation in persistence time among replicates; in 7 (identified with an asterisk) of the remaining 10 cases, the standard deviation of the mean equaled or slightly exceeded half the mean. Total consumer-presence days indicate the difference in vulnerability to invasion among treatments. When comparing treatments, there are often whole-species differences: either the species successfully colonized or it did not. For example, treatment 5 had one successful invader that persisted for less than two census periods; treatment 8, on the other hand, had seven successful invaders, some of which were long-term residents.

sisted for a short period of time. Neither of the protozoans successfully colonized in any treatment.

Between replicates within a treatment, consumers rarely differed in their ability to invade. Either the species successfully invaded all replicates, or it failed in all replicates. *Cyclops* was an exception to this rule in one treatment and persisted from introduction to the next sample period in two of four replicates. In the replicates in which *Cyclops* survived for one intercensus interval (15 d), it became extinct before the next census period. This could be considered a trivial case. Other than this instance, community vulnerability or invulnerability to invasion was perfectly repeatable. However, the time to extinction among successful invaders and the abundance of the invading species did vary among some replicates (table 7). In all but one treatment, variation in the time to extinction was never more than a single intercensus interval.

Differences in species-specific vulnerability between treatments was considerable (table 7). I use the total consumer days (defined as the sum of species persistence) per microecosystem as a measure of overall vulnerability to invasion by consumers. The total number of days on which consumer species were present varied from a minimum of 23 d for a single species in one treatment to 373 d for seven invader species in another treatment. The former treatment was clearly resistant to invasion, whereas the latter treatment was relatively vulnerable to invasion.

What factors cause one treatment to be vulnerable to invasion whereas another

treatment resists invasion? Again, controlled experiments must be conducted at each stage of assembly to establish causality. Nevertheless, correlation and comparison can suggest mechanisms, if viewed cautiously. I conducted a principal-component analysis using 23 variables, including species' invasion success, ratio of herbivores to producers, total species persistence, population-growth trajectories, sequence of species invasions, final community composition, species richness, and food-web connectance. The first three axes accounted for 88% of the data variance. The first axis (40% of the variance) ordered communities by producer dominance. The second axis (an additional 30%) ordered communities by vulnerability to invasion and persistence of consumer species. Factor loadings on the third axis (18% of the variance) were not so easily interpretable. In general, the first two axes reflected differences in species' responses to assembly sequence. In most treatments, producer dominance was determined by which producer colonized first or second in the assembly sequence, essentially a priority effect. In some cases, a herbivore that invaded early in the assembly sequence influenced this outcome and altered community vulnerability to subsequent invasions (tables 5–7).

I searched further for similarities among treatments by conducting an agglomerative cluster analysis of the invasion sequences themselves. By far, the two treatments most susceptible to invasion (8, 10) showed the highest degree of similarity of any sequential-pair clustering, at 0.5 similarity. Whether susceptibility to invasion is related to similarity in invasion sequence is unknown. No other patterns were evident in this analysis.

Timing and Sequence Effects: Large and Small Systems

To determine the influence of variation in system size and timing between invasions in the previously described results, I conducted experiments designed to control these potential effects. These experiments included reversing the period of time (10 vs. 15 d) between successive invasions in selected small- and large-system treatments. In the large systems, treatments 1 (a treatment resistant to invasion by most consumers) and 8 (a treatment vulnerable to most consumers) were used. In the small systems, treatments 1 and 3 were used, representing the two alternative states. In the small systems, there was no change in the community patterns described above when the time between invasions was increased from 10 to 15 d. When *Scenedesmus* colonized first, neither *Ankistrodesmus* nor *Selenastrum* could increase above introductory levels. This is the same result that occurred when the period between invasions was 10 d. When *Ankistrodesmus* or *Selenastrum* colonized before *Scenedesmus,* again *Scenedesmus* became dominant. However, all three species coexisted over the 80-d period in this case. Once again, these systems were vulnerable to invasion by *D. magna, Gammarus,* and *Cypris* sp.

In the large system, general trends in the assembly trajectories were not altered when the time between invasions was decreased from 15 to 10 d. The initial producer colonist again became the dominant community component. The last producer to be introduced became a relatively minor community component. When *Scenedesmus* was introduced in the large system, it could not overcome

the initial numerical disadvantage, much the same as when it was introduced using a 15-d colonization interval. Consumer species were no more successful in colonizing large treatments with a 10-d interval between invasions. Treatment 1 was again relatively resistant to invaders, whereas treatment 8 was vulnerable.

The reversal of producers' dominance as system volume increased was perhaps one of the most conspicuous trends observed in the microecosystems. Which mechanisms have the capability of reordering the strong competitive hierarchy observed in the small systems? All variables were held constant except for the period between introductions (15 d vs. 10 d), system volume (with attendant effects on available light), and changes in nutrient dynamics that were influenced by invasion sequence. I have already shown that altering the period of time between invasions had little if any influence on competitive outcomes. Furthermore, patterns of relative abundance did not vary despite changing the period of time between invasions. It seems unlikely that absolute volume itself could so drastically alter the outcome of competition given that nutrients were initially identical. Moreover, there is no apparent reason to expect any nonlinearity in competitive outcome because of volume itself.

Considering that the large and small systems also differed in geometry, variation in the distribution of light throughout the microecosystems is a likely candidate for the reduced growth rate of *Scenedesmus* in the large systems. Although both systems received the same amount of light at the surface, noticeably less light was available at the bottom of the large systems. This was due to increased absorption, refraction, and shading effects with depth (20 cm deeper than the small systems). When introduced first in the large systems, both *Ankistrodesmus* and *Selenastrum* produced large populations that made them invulnerable to the *Scenedesmus*-induced competitive depression seen in the small systems. These data suggest the numerical abundance attained at 15 d versus 10 d of competition-free population growth, coupled with lower growth rate, prevented *Scenedesmus* from becoming dominant.

DISCUSSION

Community-Assembly Mechanics

In this study, I have found that different assembly routes produce vast differences in community organization because of sequence-dependent differences in invasion success and the population dynamics of invading species. Some assembly trajectories produced communities that were resistant to invasion by consumer species, whereas other communities assembled using different trajectories were readily colonized. These dynamics occurred even though the species pool and initial environments were constant and the introduction protocol was identical among treatments. Timing, chance, and sequential effects played a powerful role in channeling community-assembly trajectories through different sets of assembly rules in the community-assembly space. Assembly rules that operate with one assembly sequence may not even be possible with another sequence. Doubtlessly, sequence-dependent changes occurred in the physical environment as

well; however, environmental changes remain to be documented. The mechanics behind community assembly generated numerous differences in emergent community properties, such as vulnerability and invulnerability to invasion, individual population-growth trajectories, and species persistence.

These results suggest a simple tenet that may be applicable to communities in general. Simply put, this tenet is that the sequence of invasions determines the set of rules that are possible and likely to operate. Such rules influence the species composition and susceptibility to invasion of the community. Different sequences exhibit different sets of assembly rules even when the species pool is held constant. This phenomenon has been explicitly supported by studies in which the invasion sequence is directly manipulated (Cole 1983; Drake 1985; Wilbur and Alford 1985; Gilpin et al. 1986; Robinson and Dickerson 1987; Robinson and Edgemon 1988) and is certainly a possible explanation in studies in which the invasion sequence is not controlled (Sutherland 1974; Sale and Williams 1982; Sale 1984; McCune and Allen 1985). In this sense, the notion that chance events and lottery dynamics govern community composition ignores the idea that, although chance may determine invasion order, rules of assembly may be determined by those invasions. Environmental variability and stochasticity may add complexity to this rule base, up to the point at which species' population dynamics are governed wholly by such variability. Of course, the vagaries of different systems most likely alter how assembly proceeds, which rules and mechanisms are significant, and the point at which environmental variability becomes significant.

To fully understand communities, one must not only have a knowledge of the extant community but also understand the historical processes that created the community. I have documented the importance of historical processes in this study. Sequence and historical effects that produce divergent communities do so because the action of these effects is influenced by chance and timing (Lawton 1987; Crawley 1989). Lawton (1987) recognized that essentially any interspecific interaction could potentially form the basis for the mechanism behind an assembly rule. In this study, I have shown that specific mechanisms (e.g., predation, competition, and emergent properties such as food-chain length) are frequently insufficient to characterize the patterns seen in ecological communities. When the actions of such mechanisms are viewed in historical terms, they become dynamically richer and are capable of producing alternative outcomes. Is it the mechanism or the historically produced variation in the expression of the mechanism that is critical to pattern formation? The mechanics of community assembly may be responsible for the production of pattern by controlling the outcome of specific mechanisms. For example, different assembly sequences are capable of creating a variety of competitive intransitivities that do not exist if species invade simultaneously (Buss 1980; Gilpin et al. 1986; this study). In fact, I have found that historical effects can create different intransitivities within the same set of species (e.g., A beats B, B beats C, C beats A; *or* B beats A, A beats C, C beats B). The switch that turns the intransitivity on or off, reversing the ordering of the intransitivity, is simply the mechanics of community assembly. Assembly mechanics include factors such as relative order of invasion, subsequent topological

properties, and sequence-dependent physical modifications of the environment. All these factors are capable of altering the action of specific mechanisms.

Deterministic and Indeterministic Assembly

During these experiments, I have found evidence for the existence of two genera of community-assembly trajectories, those that behave deterministically and those that behave indeterministically. Deterministic assembly trajectories always resulted in communities with the same producer-species composition and relative dominance and in communities that are equally susceptible and resistant to the same set of consumer species. In these assembly trajectories, there was no variation among replicate communities in terms of these properties. Most of the assembly trajectories explored here were of this type. However, indeterministic trajectories could produce alternative community end points. Essentially, treatments were not repeatable in terms of species composition, persistence, or relative dominance. In general terms, some assembly sequences contain a single attractor, given the variability that exists in the system. Other assembly sequences contain multiple attractors in the assembly state space, given individual variability. Included in system variation are factors such as minor differences in the colonizing species' growth rate and variation in founder-population clutch sizes. However, the effect of such differences in indeterministic treatments was clear: I found treatment replicates that diverged directly as a function of these differences.

What processes are capable of creating some assembly routes with multiple attractors while others have a single attractor? This can best be illustrated by considering some of the events that led to population-level "bifurcations" among replicates during community assembly. Indeterministic assembly trajectories were vulnerable to even minor variations in founder-population variables. Essentially, this is a case of founder variation being expressed along some trajectories but not others. For example, among consumer colonists, there was always some variation among the total number of embryos introduced to each replicate even though the population size of the invading adults was held constant. This variation resulted in substantially different population sizes between replicates in some treatments. A difference in a few individuals in a small population led to large differences in population size. These differences produced effects that cascaded through the community, leading to further divergence in community structure. If, upon colonization, environmental and community effects do not restrict population growth, variation in clutch size can have a large impact on subsequent community-assembly dynamics.

I illustrate the ability of founder variation to alter an assembly trajectory by considering some of the population variability observed among one of the most successful consumer invaders, *Daphnia magna*. When *D. magna* invaded any treatment, only individuals carrying embryos were introduced. Treatment 8 was an assembly sequence that proved to be particularly vulnerable to invasion by consumer species. *Daphnia magna* was the first consumer species to invade the system, which at that time contained only *Chlamydomonas* and the two species of bacteria. When *D. magna* was introduced, the abundance of *Chlamydomonas*

among replicates was virtually identical (mean = 2.5×10^6 cells mL^{-1}, SD = 2.31×10^3, $n = 4$). Because no other species had yet invaded, *D. magna* colonized replicates that had essentially identical environments. At the next census period 15 d later, there was considerable variation in the number of *D. magna* among replicates. Forty-five days after *D. magna* invaded, there were more than 430 individuals in one replicate and 9 in another. Variation in the number of individuals that survived to reproduce and differences in clutch size among the founder populations appear to be responsible for the differences in population growth among replicates in some treatments. Other assembly sequences in which *D. magna* was a long-term resident were not vulnerable to founder effects.

Differences in grazing pressure were responsible for variation in the invasion success of some producer populations. For example, *Ankistrodesmus* was the third invader in treatment 8, and it was rare in the replicate that supported the largest *D. magna* population. In this replicate, it rapidly fell two orders in magnitude from its introduction density (from 10^4 cells mL^{-1} to $<10^2$ cells mL^{-1}). Conversely, in a much less heavily grazed replicate, *Ankistrodesmus* became the dominant producer species (exceeding 10^6 cells mL^{-1}). In this treatment, the population abundance of *Chlamydomonas* did not differ significantly among replicates during the course of community assembly. This may be due to the inability of *D. magna* to depress large *Chlamydomonas* populations at the population levels attained during this study.

In deterministic treatments, variation in the number of embryos had little effect on the ultimate population size of the invading species. Variation in founder characteristics was not expressed in such treatments. This result was due to constraints on invader population growth imposed by community and environmental properties at the time of invasion. In some cases, this result was due to suppression of the growth rate of the invading species. For example, I found treatments in which producer abundance was strongly controlled by large populations of grazers. In these treatments, grazing pressure did not allow divergence among replicates. Smaller populations of grazers did not have nearly as great an impact on invading producers. In such cases, divergence was possible. Of course, a producer system resistant to all invading herbivores (treatments 4, 5, 6) is entirely immune to consumer-induced effects.

Assembly Rules and State Space

The ability of the process of community assembly to alter the outcome of strong deterministic interspecific interactions suggests a need for careful reevaluation of the relationship among patterns, mechanisms, and assembly mechanics in ecological studies. In nature, differences among invasion sequences, and subsequent assembly trajectories, are historically derived and often due to chance colonization events (Allen et al. 1977; Abrams et al. 1985; Drake 1985; Gilpin et al. 1986; Robinson and Dickerson 1987; Robinson and Edgemon 1988; Crawley 1989). Can we understand the factors that are responsible for community structure when we lack information about assembly history? Unfortunately, the answer is equivocal: sometimes yes, but only under special circumstances; for the most part, no. In most community studies, we uncover the mechanisms responsible for *main-*

taining the extant community. However, there is no guarantee that these mechanisms are ultimately responsible for community structure.

I illustrate this crucial point with an example. Several of the assembly trajectories converged or crossed at one or more points during the course of community assembly. That is, there were treatments that had the same species composition and relative abundance in all replicates at some time during assembly. Such systems, although assembled by different routes, appear similar. In such cases, it is reasonable to compare the behavior of such communities without information about assembly history. This is essentially what is done in comparisons of the structure of extant communities in nature. Consider a point along the assembly trajectories of two communities (treatments 6 and 10 in this case) where organization appears identical. At this point, it was impossible to distinguish between the two communities: they looked the same, and their topological representations were identical. Subsequent to this stage, both communities were invaded by *Cyclops*. In treatment 6, this invader was unsuccessful, persisting for only a single intercensus interval in one replicate and becoming extinct in the remaining replicates before the first postinvasion census. However, in treatment 10, this invader successfully colonized the communities and became a long-term resident. If indeed the communities were identical, there is every reason to believe they should be vulnerable to invasion by the same species. Despite clear structural similarities, these communities responded differently to invasion.

The implications of this type of behavior are enormous. Given limited information (e.g., snapshots of the extant communities, often all the information we have in even long-term studies), one may conclude, as suggested by Simberloff and colleagues (see Strong et al. 1984), that an explanation based on chance alone adequately explains observed patterns. As a result, community organization is likely to appear idiosyncratic. However, given additional information (e.g., information about the system's assembly history), it is clear that this can be a gross misinterpretation. Although I have not yet conducted controlled experiments to explore the source of this differential vulnerability to invasion, it is clear that these communities are different in many regards, given information about the entire assembly trajectories. Whether the extant community is composed of species that are increasing or decreasing in abundance, their relative physiological state, environmental changes induced by species no longer present, and many other such factors can influence invasion success. The community-state vectors (e.g., conditions found in the extant community) are not always adequate to evaluate wholly the resulting community. To understand ecological systems, we must not only be able to "take apart" communities and understand how they reassemble, as suggested by Gilpin et al. (1986), we must also understand the potentially powerful role that historical events play in community-assembly mechanics.

Although the kind of information required to distinguish between mechanism and chance in nature is difficult to obtain, I have demonstrated that such information can be essential if we are to attribute cause to pattern. Furthermore, community patterns produced by deterministic processes can appear highly variable or even stochastic when little information about the trajectory that produced that

community is available. It will not be simple to attribute pattern to mechanism, or to understand the apparent lack of pattern, without considerable historical information.

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