To the Graduate Council:

I am submitting herewith a dissertation written by Gary Robert Huxel entitled "Influences in Community Assembly." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

James A. Drake, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

Influences In Community Assembly

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Gary Robert Huxel
December 1995

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Acknowledgements

The completion of this work would not have been possible without the help and support of a number of people. The faculty, staff, and graduate students in the Graduate Program in Ecology have provided me with much insight, encouragement, laughter, and support of various kinds. I am especially grateful to those who have served as Dissertation committee members throughout my five years at the University of Tennessee. Dr. Dewey Bunting has been particularly supportive of me during my stay with both finances and his friendship. Cornell and Linda have put up with my last minute I need's and kept me in line. I have often been asked what's it like to work for Dr. James A. Drake, and my usual reply is "He's a real pain, but one who has really made me think and ask questions. His ability to put up with me is awe inspiring."

I would also like to thank my dissertation committee members Michael McKinney, Gary Sayler, and Michael Huston. A number of faculty members here and elsewhere have been most helpful. Without the insight of Chad Hewitt I would probably still be floundering about. Thanks also to Greg Witteman and to the graduate students in the Life Sciences and others I have been associated with at the University.

Of course, I am most in debted to Cheri Sue LaRue, whose guidance, support, encouragement, and love has helped me maintain a balance of life.

Abstract

This dissertation is a collection of four bodies of work which have focused on issues of processes and mechanisms that influence ecological systems. The distribution and abundance of species is the central issue of ecology. To persist in the natural environment, species must coexist with other species in environments that may be periodically perturbed so that ecological systems are constantly undergoing change at some scale. Thus, ecological systems are dynamical and assemble within the bounds of certain rules. In the first of these works, the dynamics of overlapping perturbations is examined. Perturbations of the "1/f" distribution type were placed onto a model landscape. Collapses occurring from the perturbations were independently placed on the landscape and the resulting dynamics were examined. It was found that these overlapping perturbations led to a range of distributions depending on the number of perturbations and their spectral coefficients. In the second study, four green algal species were studied to examine the influence of invasion sequence and timing. A competitive hierarchy was established based upon phosphorus use efficiency. It was found that this hierarchy could be altered by varying the sequence and timing of species inoculations, as well as by varying the inoculation densities and various environmental factors of the system. The last two studies involved the modelling of community assembly. Again, invasion sequence was found to alter the community dynamics of a model system. Several previous assembly models had two key assumptions,

single invaders and low inoculation densities, built in which led to the development of complete invasion resistance. When these two assumptions were relaxed, it was found that invasion resistant states did not occur. However, invasion resistance was found for most species and increased numbers of invading species resulted in increased turnover.

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CHAPTER 1

Introduction and Overview

Introduction

The assembly of ecological communities is a result of a series of invasion and local extinction events that may involve one or more species per event (MacArthur and Wilson 1963, 1967; Simberloff and Wilson 1969; Diamond 1975; Dickerson and Robinson 1985b; Drake 1990a). The assembly process may lead to either recurrent turnover in species composition (non-equilibrium dynamics), to invasion resistant states (equilibrium dynamics), or even cycle among states (complex attractor with multiple alternate states) (Robinson and Dickerson 1984, 1987; Hengeveld 1986; Drake 1991). Factors that determine whether a community attains invasion resistance or experiences continual change in species composition involve the properties of the community being invaded, the invading species, and environmental conditions (Elton 1958). Elton predicted that communities develop increasing invasion resistance as their food web structures become more tightly connected and as a logical extension, complete invasion resistance may arise. Tighting of connections occurs when competition increases as niche partitioning becomes increasing finer. Whether complete invasion resistance occurs or not, is then a function of local processes of competition, predation, and other

species interactions and regional processes of migration (invasion, colonization) and speciation (Ricklefs 1987; Ricklefs and Schluter 1993).

The question of whether communities reach an uninvadable state or not is part of the older problem of stability (i.e. the "balance of nature"). The balance of nature argument is one that has dominated much of ecological research over the years. Since the 1950's the debate concerning community stability has been largely been rooted in arguments over whether complexity, mainly in the form of species numbers, increases or decreases stability. Earlier theoretical studies suggested that stability increases with complexity (Odum 1953; MacArthur 1955). While other studies have argued that either the inverse relationship may hold (May 1973) or that there is no clear relationship (Maynard Smith 1974; Goodman 1975).

To further address the question of community stability, randomly created linearized community matrix models of the Lotka-Volterra equations have been developed (Robinson and Valentine 1979; Post and Pimm 1983; Drake 1990b; Hewitt et al. in prep). In the earlier studies of stability (May 1973; Maynard Smith 1974; Goodman 1975), the manner of selection of the random state variables drove the dynamics of the system, so that by altering the range of values allowed, stability could either increase or decrease with complexity. Robinson and Valentine (1979) stated that much of the confusion over how complexity influenced stability rested in the way in which stability was defined. The typical definition of stability was the constancy of species composition in a community. Robinson and Valentine (1979) suggested that invasion resistance was

also a factor in community stability. To test this, they subjected randomly created communities to invading species and found that invulnerability to invasion increased with complexity while stability decreased. Thus, the two natures of stability were oppositely related.

Following the work of Robinson and Valentine (1979), a number of similar community matrix models were developed to address the issue of stability and invasion resistance in successional communities. These models involved sequential invasion attempts by a randomly selected species each time step. Post and Pimm (1983) found that in their model system the number of species eventually leveled off, but did not stop increasing, given an infinite pool. However, they did not allow the successful invasion of any species that caused the lost of other species. Ginzburg et al. (1988) found that in a community of competitors a completely invasion resistant state would be reached. Drake (1990a, 1991) and Hewitt et al. in prep found that using a finite species pool and allowing one species to attempt to colonize each time period led to a number of uninvadable community states that arose given different random assembly sequences.

While the majority of these theoretical approaches supported the Eltonian view (Elton 1958) that complete invasion resistance would develop in communities as structure within them formed, numerous field studies demonstrated that this was not always the case. Many field studies show that many communities are constantly losing and gaining species, while the usual exceptions to the dynamical community are isolated systems. In fact, Elton (1958) even suggested that in "open" communities invasion and extirpation

would be common. Moreover the very notion of community succession being cyclic (Odum 1969) demonstrates that invasion resistance should be a relative term and community dynamics are in part driven by historical processes. For example, studies of coral reef fishes Sale (1977, 1978) and sessile marine organisms (Fagerström 1988) demonstrate that in those systems, succession is driven almost exclusively by chance (lottery succession).

Historical factors contributing to the development of community structure have been most often examined from the perspective of relatively rare events. Species arrivals (or colonizations) have been assumed to occur infrequently and as a consequence independently. This consideration has extended to the assumptions underlying many of the assembly models. The sequence of species additions and timing of arrivals have been shown to have great influence on community structure (Robinson and Dickerson 1987; Case 1990, 1991; Drake 1990a, 1991; see also Chapter 2). These results may be due to the influence of "priority effects" (Alford and Wilbur 1985) or the action of transitive competitive interactions which alter the direction of the assembly trajectory (Barkai and McQuaid 1988).

Species have been described in terms of the timing of their establishment into communities, with some lumped as "weedy" or early successional species and others as "climax" or late successional species with a whole spectrum of possibilities in between the two extremes (Drury and Nisbet 1973; Grime 1979). Within these categories however, historical or "priority" effects such as the sequence and timing of invasion may

alter competition abilities between species leading to intransitivities (Harper 1961; Dickerson and Robinson 1985b; Robinson and Dickerson 1987; Drake 1990b, 1991; Drake et al. 1993). This may lead to the "forbidden combinations" of Diamond (1975) or the "home field advantage" described by Pimm (1989). Additionally, species intransitivities are known to occur due to environmental conditions (Park 1954; Gilpin and Case 1976; Tilman 1977, 1982, 1993; Gilpin et al. 1986).

While the effects of sequence and timing of species invasions on community dynamics have been explored, the rates of invasions have been essentially neglected. Theoretical studies including assembly models and island biogeography theory (MacArthur and Wilson 1963, 1967) both assume that colonization events are rare, so that species essentially invade singularly. However, many studies have shown this assumption to be violated. Elton (1958) stated that some systems will remain open experiencing high rates of colonization and extinction.

Mainland communities may closely follow the dynamics of open systems, while island communities may follow those of closed systems. Open communities are considered to be stochastically dominated systems in which the attributes of the individual species are solely responsible for determining community membership (Gleason 1926; Sale 1977, 1978). Thus there is no long-term historical component to species membership. In contrast the concept of a closed community suggests that the structure of the extant community contributes to determining the membership of a colonist. This approach to community development, dubbed the *balance of nature*

paradigm (Clements 1916; Elton 1958), suggests that communities assemble towards a stable, equilibrial, invasion resistant state.

Undoubtedly the true nature of communities lies somewhere in between these two extremes. Thus in order to understand the structure of an extant community the historical process of assembly, the assembly trajectory, must be considered (Drake 1990b; Drake et al. 1995). The rate, sequence, and timing of arrivals have been shown to have great influence on community structure by regulating species membership through either facilitation or inhibition (Connell and Slatyer 1977; Robinson and Dickerson 1985; Case 1990, 1991; Drake 1990a, 1991; see also Chapter 2). In addition, extinction dynamics are important in the development of ecological systems. Species extinctions and disturbances are known to follow power-law (hollow curve) dynamics (Raup 1986, 1991; House 1989; Drake et al. 1992; Milne 1992; Hewitt et al. in prep; Kolasa et al. in prep). To address these issues, I present four papers in three parts.

In Chapter 2, to understand the mechanics of competition and species coexistence, I examined the ways in which competitive outcomes among four species of green algae (*Scenedesmus quadricuada, Selenastrum capricornutum, Chlamydomonas reinhardti, Ankistrodesmus falcatus*) could be transposed under different invasion sequence, timing, and inoculation densities. Differences in invasion sequence, timing, and inoculation were all capable of producing alternative community states, expressed as differences in either species composition or relative abundance. Manipulation of the physical environment was also performed to examine the role of changing environmental conditions on

assembly processes. Continuous mixing led to different assemblage dominance patterns as opposed to sporadic mixing or no mixing at all. Nutrient media was manipulated by allowing each species to grow axenically, followed by filtration, and using this filtered media as experimental media. Differences in media source lead to differences in assemblage composition and dominance. Continuous addition of nutrients into microcosms lead to greater species coexistence than did no addition. These results suggest that alternative assemblage states are possible given differences in invasion sequence, timing, and inoculation as well as differences in environmental conditions.

In Chapter 3, my objective was to test whether the independent relaxation of two of the assumptions of assembly models, single colonizers and low density of colonizers, would limit invasion resistance. Specifically in the first chapter of this part, in some simulations two species were allowed to attempt to colonize each time step and in other simulations I removed the increase when rare test. The relaxation of the second assumption allowed the colonizers to invade at Lotka-Volterra equilibrium densities. These relatively simple questions may have many consequences on the dynamics of community assembly and therefore, on community level theory as a whole. Differences between island and mainland systems have been noted, while many community theories have depended on dynamics in island systems (Diamond 1975; Brown 1971). It is suggested that differences between these two types of systems in terms of invasion resistance may be due to the relative rates and numbers of colonizers/invaders.

In Chapter 4, immigration and its effect on community assembly are examined. The theory of island biogeography suggests that species diversity is a result of dynamic equilibrium between colonization and extinction. MacArthur and Wilson proposed that colonization is driven by proximity to a species pool, whereas extinction is a random process largely related to population size. Conversely, invasion theory suggests that colonization success and extinction events are driven by attributes of both the extant (recipient) community and the invading species. Using a community assembly model, I attempt to provide a link between the two theories by examining the influence of increasing numbers of immigrating species on invasion dynamics. I found that increasing the number of species that simultaneously immigrate results in increased colonization, extinction, and consequently turnover. Thus, increasing the number of immigrating species may make communities more susceptible to invasion. This seems to be most important for systems that are now, but have not historically experienced high immigration rates.

In Chapter 5, the dynamics due to the potential for overlap among perturbations are examined. Numerous physical and biological systems appear to exhibit temporal dynamics which have 1/f or power-law distributions with spectral coefficient values (ω) ranging from zero to two. The tacit assumption has been that the 1/f signal arises as a consequence of a single mechanism or process. In many systems however, the observed dynamics may be the result of multiple interacting processes, each independently exhibiting a $1/f^{\omega}$ signal. In such situations the resulting distribution has two contrasting

theoretical formulations: the multiplicative property of power-laws or the generalized gamma-distribution. Employing a landscape model in which multiple interacting signals (for ω=0.5, 1.0, 1.5, 2.0, and 3.0) induce patch disturbances, I find that the aggregate spectral coefficient does not follow the predicted behavior of the multiplicative power-law model. Instead, as the number of interacting $1/f^{\omega}$ perturbations increases, the frequency-magnitude relationships exhibit increasing departures from power-law attributes. The mode of the resulting relationships shift increasingly toward the right, exhibiting a closer approximation to the gamma-distribution. These results suggest that the power-law may provide an inadequate description of the dynamics of multiple, interacting perturbation systems. Instead the gamma-distribution appears to be a better descriptor of the underlying dynamics.

Overview

Together, these studies suggest that a multitude of complex dynamics can and do occur in natural systems. Assembly can lead communities in a variety of directions depending upon random events and deterministic interactions. Given this, what direction should ecology take. One direction that I believe is a examination of complex dynamics across scales. Brown (1995) suggests that it may be impossible to predict exact trajectories of populations or communities, however the boundaries of these systems may be detected. For instance, in Chapter 4, I show that stochastic boundedness of assembling

systems may be violated given significant levels of immigration. However, within that system there are deterministic rules such a predator must be in a system where its prey species is present to survive.

Thus, one must know how systems operate across various scales. Kolasa et al. (in prep) have shown in their system of natural rock pools species follow a hollow curve in terms of abundance and distribution. So that most species are rare both in numbers and numbers of sites occupy. These species contribute greatly to species extinction rates which follows a hollow curve distribution. Taken with the high rates of turnover found in my model systems with increased immigration (both species and numbers of individuals) these rare species may contribute greatly to turnover dynamics without greatly affecting the community structure. Thus, rare species need to be either long-lived or able to disperse relatively fast in terms of competition, predation, and other perturbations.

Fox and Fox (1986) found that biological invasions have not occurred in Australia without some kind of disturbance. However, Australia has experienced low rates of immigration historically. The results in Chapters 3 and 4 suggest that increased immigration will lead to greater incidences of invasion of exotic species. Thus, given the high rates of turnover in mainland systems and increased rates of human mediated movement of exotic species, many rare species are in grave danger of becoming extinction outside of zoos and botanical parks.

CHAPTER 2

Intransitive Interactions Among Four Green Algal Species

Introduction

Communities are assembled structures, deriving pattern from an interplay between historical inertia and the action of contemporary processes (Drake 1990a, 1990b, 1991; Drake et al. 1993, 1994). As a community assembles, ecological processes vary spatially and temporally in their occurrence, intensity, and contribution to the regulation of structure. Initially numerous assembly trajectories are possible, however as assembly proceeds each historical event directs or attracts the system into specific regions of the community composition state space. Trajectories which produce alternative community states may either be deterministic or indeterministic. Deterministic trajectories approach specific community states leaving little room for variation in organization, while indeterministic trajectories are susceptible to slight differences in assembly (e.g., minor skews in the sex ratio of an invading population). Specifically, herein I examine the roles of the sequence and timing of species invasions and variability in environmental conditions in the development of alternative community assembly trajectories and community states.

Assembly processes are capable of enhancing regional species coexistence through the production of alternative states (Hutchinson 1961; Pimm 1982; Ricklefs 1987; Drake et al. 1993). Such dynamics, integrated with the classic mechanisms (e.g., competition and predation) of ecology, offers the promise of a robust understanding of community (Tilman 1977; Paine 1966; Connell 1961). Assembly processes can add significant dynamics to the operation of virtually all ecological and evolutionary processes. However, it is not always sufficient to know which mechanisms and processes operate in a community. A more complete understanding of community level dynamics and structure comes from knowing how the mechanisms and processes vary in significance or strength as communities assemble. For instance, competition between two algal species for nutrients will be a weak force if predation keeps competitor densities low relative to available nutrient levels. While predation mediates competitive interactions under specific conditions (Paine 1966, 1974), a decline in predator abundance may functionally switch-on competition between prey species. Resource competition may then increase in importance to a level where it becomes the dominant type of interspecific interaction, resulting in changes in species composition through competitive exclusion (Paine 1974).

Here, I limit this study to a few assembly processes which are capable of reversing or overriding competitive outcomes. These dynamics serve to produce alternative community states which, when spatially extended, permit the long term coexistence of species and generation of regional biodiversity. In addition, while Drake

(1991) and Robinson and Dickerson (1987) showed that invasion sequence played a strong role in the production of alternative community states, neither of these studies were designed to uncover the mechanisms which were responsible for the production of alternative states. Using highly controllable laboratory microcosms I conducted six sets of experiments (Table 1) each of which explored a different aspect of the community assembly (Harper 1961; Robinson and Dickerson 1987; Dickerson and Robinson 1985b; Drake 1990b, 1991; Drake et al. 1993). In particular, I looked at situations that potentially lead to transitions between community states during the course of community assembly. Of principal interest is ascertaining whether changes in any of six variables (invasion sequence and timing, water column mixing regime, chemical history of the environment - filtrates, invasion abundance, and nutrient inputs) are able to produce alternative states among communities assembled from a fixed species pool. My ultimate objective is understanding the manner in which competitive dominance hierarchies can be subverted by assembly processes.

Materials and Methods

General Methods

Six sets of experimental manipulations (Table 1) were carried out, designed to study several parameters involved in the mechanics of assembly using a planktonic algal

assemblage as a model. Four species of green algae (Chlorophyta) obtained from the University of Texas culture collection (UTEX) were used: *Scenedesmus quadricauda* (Turp.) [Bréb.] (UTEX 76); *Selenastrum capricornutum* (Printz) (UTEX 1648); *Chlamydomonas reinhardtii* P.A. Dang. (UTEX 2246); and *Ankistrodesmus falcatus* (A. Br.) [G.S. West] (UTEX 101). These species were chosen due to previous experience with them as model species and the ease of culturing them in the laboratory. All species are unicellular; but, *Scenedesmus quadricauda* forms coenobia of four or eight cells.

All experiments were conducted in parafilm-covered 250 mL or 1000 mL Erlenmeyer flasks housed in an environmental growth chamber. The cultures were checked weekly to insure that they were axenic. The chamber maintained a constant temperature (18°C) and photoperiod (12L:12D) throughout the experiment. A standard chemically defined medium for phytoplankton was used (Appendix, Drake et al. 1993). Unless otherwise noted, no nutrient additions were made after an experiment was begun. Log-phase cultures grown under the same environmental conditions as used in the experimental procedures, were used as inocula. Log-phase growth occurred from day 7 to day 14 for all species (unpublished data).

Species abundances within cultures and treatments were monitored by stirring each microcosm and removing a 1mL aliquot with a Pasteur pipette;. 1mL of fresh medium was added as replacement. Density (cells/mL) was determined by counting a total of 500 algal cells (cells of all species) using a Palmer-Molony counting chamber (Wetzel and Likens 1991). The lower detection limit using this procedure was a density

of 100 cells/mL. The chamber was completely scanned in cases where cell density dropped below 100 cells/mL to track population density as they became rare.

Nitrate+nitrite nitrogen, ammonium, and soluble reactive phosphorus were analyzed by spectrophotometric techniques using a Milton Roy Spectronic 401. Nitrate-nitrite concentration was determined by the diazotization method (Wetzel and Likens 1991). Soluble reactive phosphate was determined by the ascorbate-molybdate method (Lind 1979). Ammonium was determined by the Nessler reagent method (American Public Health Association 1974).

In all experiments, each treatment was replicated three times unless noted otherwise.

Experiment 1 - Growth rates and resource utilization

The objective of this first set of experiments was to measure growth rates and resource uptake rates, and to estimate resource use efficiencies for each species. The species were ranked on the basis of utilization efficiencies of phosphorus, the most common limiting nutrient in many freshwaters (Vollenweider 1968, 1975; Schindler 1978). Single species growth rates were measured in axenic cultures started in 250 mL Erlenmeyer flasks at a density of 10^4 cells/mL. Cultures were sampled for cell density and nutrient (N, P) concentrations after 10, 18, and 25 days of growth. Nine replicates were established for each species, three of which were sacrificed for nitrogen and

phosphorus analyses at each sampling period. Average growth rates and P depletion rates were determined for each time interval. The resource utilization efficiency (RUE) calculations were made by dividing the number of cells produced by each species by the amount of P used up during the time interval.

Experiment 2 - Invasion sequence and timing

The objective of the second experiment was to determine whether alternative competitive outcomes (intransititive dynamics) arise when the timing and sequence of invasion was altered. No nutrient additions were made after the experiment was initiated, hence N and P were likely depleted over time. I have manipulated the periods between invasions and the invasion sequence to examine their influence on community assembly. Three sets of experimental treatments were run in which the amount of time between invasions and the sequence of invaders was altered. Inter-invasion intervals were manipulated at three levels: zero days (simultaneous invasions), ten days, and fifteen days (cf. Drake 1991). In the latter two treatments, invasion sequences were designed to allow each species to be introduced first. Species were introduced at densities of 10^4 cells/ml. These treatments were terminated 10 days after the last species invasion. The simultaneous invasion trial was run for 40 days.

Experiment 3 - Invasion inoculation density

This experiment explored the role of inoculation density on competitive interactions between species. An increase in inoculation density of the invader could either greatly accelerate the increase in population size increase or provide a buffer for the invading species to become adjusted to the new conditions thus reducing the risk of invasion extinction. This was accomplished by repeating both the 10 and 15 day interval sequence treatments from experiment 2, while varying the invader density. Each species was introduced at the density comparable to 10 or 15 days of growth starting from 10^4 cells/ml (from experiment 1). Additionally, the invasion sequence was altered for each invasion interval in a fashion identical to that used in experiment 2. All experimental treatments were terminated after 60 days.

Experiment 4 - Filtrate interactions

Many algal species are known to exhibit allelopathy, the production of secondary metabolites that inhibit the growth or activity of competitors, decomposers, and herbivores (*e.g.* Muller 1966; Bartholomew 1970; Whittaker and Feeney 1971). A set of three treatments was established to discern whether secondary metabolites acting as allelochemicals are potentially involved in regulating interactions among the species used in this study. Additionally, many species are known to alter nutrient levels and ratios in a

way that leads to a reduction in the growth of potential competitors. Here, I ask whether there is evidence for allelopathic compounds or nutrient alterations which impact the population growth of competitors.

To address whether the allelochemicals were affecting growth in single species cultures, each species was exposed to medium modified by the metabolic products from all species. Thus, any allelochemicals produced would be present in the medium despite the absence of the cultured species. Medium was prepared by filtering axenic cultures of each species after 15 days of growth. Nitrogen and phosphorus were adjusted to full strength levels in the filtrate. Each species was inoculated into medium from all four species species and allowed to grow axenically for 10 days.

The effect of allelochemicals on assemblage dominance was examined by exposing each species to medium modified by the metabolic products from all species. The medium was prepared as in the first treatment. Medium from each species was then reinoculated with all four algal species simultaneously at a density of 10^4 cells/mL and evaluated for 40 days.

To separate out the influence of nutrient alteration in the presence of metabolites, nitrogen and phosphorus concentrations were adjusted in the filtrate to full strength medium levels before the algae were reinoculated. In this treatment, all four species were introduced simultaneously and allowed to grow for 40 days.

Experiment 5 - Water column mixing

The objective of the fifth experiment was to examine whether water column mixing altered competitive outcomes (Sommer 1991). Does community development differ between continuously mixed and unmixed microcosms? Reynolds (1993) found that the frequency of lake mixing events altered successional trajectories of pelagic phytoplankton. Mixing or stirring limits the ability of species to form the aggregated clumps of individuals known to occur for many planktonic algal species. Such aggregation may result either from the physiology of the organisms or from redox potential changes in the system. Clumping limits nutrient uptake of individuals and may alter sinking rates. Increased sinking rates causes a buildup of individuals on the bottom of the microcosms and may result in localized nutrient depletion. In the above Experiments 1 through 4, each culture was stirred twice a day, here all cultures were continuously stirred. All species were simultaneously inoculated at densities of 10^4 cells/mL. This experiment was conducted for 40 days.

Experiment 6 - Continuous flow

In this experiment the role of continuous medium input on competitive outcomes was evaluated (Vollenweider 1975). Continuous medium input decreases nutrient depletion and buffers pH levels, in contrast to conditions in static microcosms.

Phosphorus and nitrogen levels were found to drop to nearly zero, as biomass accumulated under static conditions (Experiments 1 through 5, unpublished data), in most cases within ten days of inoculation. Such severe nutrient depletion should increase the level of competition for the limiting nutrient. The species that can utilize a resource at its lowest level should always competitively exclude other species in cases were nutrient levels are depressed below a species tolerance level (Tilman 1982). Additionally, pH increases dramatically over time in the static microcosms approaching 10 during the light period due to CO_2 uptake during photosynthesis. Addition of buffered medium should limit these increases.

Full strength medium was continuously pumped into 1-Liter flow microcosms at a rate of 250 mL per day using a peristaltic pump. This volume represented 25% of the total volume being turned over each day (cf. Tilman 1977) simulating a 25% population mortality per day for each species. As a control, all four species were inoculated simultaneously at densities of 10^4 cells/ml, while the treatments had 10 day intervals between invasions. The first treatment had an invasion sequence of *Chlamydomonas*, *Selenastrum*, *Ankistrodesmus*, and *Scenedesmus*, while the second treatment had an invasion sequence of *Ankistrodesmus*, *Scenedesmus*, *Selenastrum*, and *Chlamydomonas*. These sequences were selected based on results from experiment 2 in which the sequences produced alternative states in unstirred conditions. This experiment was run for 63 days and four replicates of each treatment were run.

Results

Experiment 1 - Growth rates and resource utilization

For a 10 day period, *Chlamydomonas* and *Selenastrum* had the highest mean population growth rates (0.626 cells/day and 0.605 cells/day, respectively). *Scenedesmus* had a lower mean growth rate (0.295 cells/day), while *Ankistrodesmus* had the lowest mean growth rate (0.095 cells/day) (Table 2). (Note that Table 2 gives average growth rates (dN/dt), resource (phosphorus) uptake rates (dR/dt), and resource utilization efficiencies (RUE) for varying time intervals of growth (10 day, 18 day, and 25 day) for the four axenically growing species of green algae. Different letters indicate significant differences at the p=0.05 level between column values, while the same letter indicates no signifcant difference.) Mean growth rates were not significantly different between *Chlamydomonas* and *Selenastrum* ($F_{[3]}$= 0.14, p>0.05)(Table 2), however the growth rate of *Scenedesmus* was found to be significantly different from both *Chlamydomonas* and *Selenastrum* ($F_{[3]}$= 74.16, p<0.05 and $F_{[3]}$= 27.28, p<0.05, respectively), but not from *Ankistrodesmus* ($F_{[3]}$= 4.72, p>0.05). The mean growth rate of *Chlamydomonas* declined from its 10 day value to the 18 day period (0.369 cells/day). *Selenastrum*'s mean growth rate also was lower over the 18 day period (0.365 cells/day) than over the 10 day period. *Scenedesmus* had its highest mean growth rate for the 18 day period as its mean growth rate increased from 0.295 cells/day to 0.401 cells/day. This was also the highest mean

growth rate of the four species for the 18 day period. *Ankistrodesmus* had its highest growth rate for the day 18 period (0.326 cells/day). *Scenedesmus*'s mean 18 day growth rate was significantly greater than those of *Chlamydomonas* and *Ankistrodesmus* ($F_{[3]}$= 24.96, $p<0.05$ and $F_{[3]}$= 131.35, $p<0.05$; respectively), but not significantly different from *Selenastrum* ($F_{[3]}$= 7.39, $p<0.05$)(Table 2). For the 25 day period, *Selenastrum*'s mean growth rate had once again become significantly greater than *Scenedesmus*, *Chlamydomonas*, and *Ankistrodesmus* ($F_{[3]}$= 17.98, $p<0.05$, $F_{[3]}$= 64.10, $p<0.05$, and $F_{[3]}$= 20.48, $p<0.05$; respectively). *Scenedesmus* and *Ankistrodesmus* had dropped to their lowest level at the 25 day period (0.223 cells/day and 0.201 cells/day; respectively), with no significant difference between their growth rates($F_{[3]}$= 2.70, $p>0.05$). *Chlamydomonas* had the lowest mean growth rate of any species for the 25 day period (0.166 cells/day) significantly less than both *Scenedesmus* and *Ankistrodesmus* ($F_{[3]}$= 24.96, $p<0.05$ and $F_{[3]}$= 81.25, $p<0.05$; respectively). Thus, *Chlamydomonas* went from the highest mean growth rate of the four species for the 10 day period, to the lowest for the 25 day period.

Average RUE increased from the 10 day period to the 18 day period for all species, but then declined from the 18 day period to the 25 day period. This initial RUE increase was due to a decreased rate of resource depletion (Table 2). The decrease in RUEs for the 25 day period versus the 18 day period, was a reflection of depressed growth rates due to resource depletion.

A resource use hierarchy based upon the 10 day phosphorus use efficiency was established in which *Selenastrum* had the greatest mean RUE, but not significantly different from *Chlamydomonas* ($F_{[3]}$= 1.46, $p>0.05$). *Scenedesmus*'s RUE was significantly less than *Chlamydomonas*'s ($F_{[3]}$= 49.44, $p<0.05$) and greater than, but not significantly different from, that of *Ankistrodesmus* ($F_{[3]}$= 3.329, $p>0.05$). The RUE hierarchies were different for the 18 and 25 day periods (Table 2). For both the 18 day period, *Selenastrum*'s and *Scenedesmus*'s RUEs were not significantly different ($F_{[3]}$= 1.63, $p>0.05$). *Chlamydomonas*'s RUE was significantly less than both *Selenastrum*'s and *Scenedesmus*'s ($F_{[3]}$= 9.95, $p<0.05$ and $F_{[3]}$= 78.39, $p<0.05$; respectively), but was significantly greater than that of *Ankistrodesmus* ($F_{[3]}$= 36.45, $p>0.05$). For the 25 day period, *Scenedesmus*'s RUE was significantly greater than that of the other three species (Table 2). *Ankistrodesmus*'s and *Scenedesmus*'s RUEs were not signifcantly different ($F_{[3]}$= 2.69, $p>0.05$), but both were significantly greater than that of *Chlamydomonas* ($F_{[3]}$= 20.50, $p<0.05$ and $F_{[3]}$= 67.10, $p<0.05$; respectively).

Experiment 2 - Static invasion sequence and timing

The time interval between successive invasions greatly influenced the outcome. *Scenedesmus* was always the competitive dominant in the 10 day inter-invasion interval treatment (Table 3). When the invasion interval was zero days (simultaneous inoculation), *Scenedesmus* rapidly became dominant and either drove competing species

extinct or severely reduced their abundance (Table 3). However, when the invasion interval was increased to 15 days, the first species inoculated always became dominant except when *Chlamydomonas* was inoculated first (Table 3). In those cases, the species which invaded immediately after *Chlamydomonas* (the second invader) became the numerical dominant.

Experiment 3 - Invasion inoculation density

Inoculation density did not appear to influence the outcome of competition between species. Despite the different inoculum densities for each species due to differences in growth rates, *Scenedesmus* always became dominant in treatments with 10 day invasion intervals. This result matched the 10 and 15 day invasion interval treatments of Experiment 2. However, when the time between invasions was increased to 15 days for both inoculation density levels (representing 10 and 15 days of growth, respectively), the first species introduced always became dominant, including *Chlamydomonas* (Table 3).

Experiment 4 - Filtrate interactions

In the treatment in which the filtrate medium was not readjusted to full strength and species were inoculated simultaneously (Table 3), *Chlamydomonas* rapidly became dominant (density exceeding 10^6 cells/mL) regardless of filtrate source. *Ankistrodesmus*

persisted throughout the experiment, but was unable to increase much above its initial invasion density. The growth rates of *Scenedesmus* and *Selenastrum* were greatly reduced and both species were rapidly driven extinct.

In the treatment in which the medium was readjusted to full strength and all four species introduced simultaneously, *Chlamydomonas* became the numerically dominant species in some replicates and *Scenedesmus* was dominant in the other replicates. Both *Scenedesmus* and *Chlamydomonas* exceeded densities of 10^5 cells/mL in each replicate, while *Ankistrodesmus* and *Selenastrum* never attained densities of 10^5 cells/mL.

In the treatment in which the nutrients were readjusted, *Scenedesmus*, *Ankistrodesmus*, and *Selenastrum* growth rates were depressed in filtrate from *Chlamydomonas* in contrast to growth in their own filtrate (Table 4). *Chlamydomonas*, *Ankistrodesmus*, and *Selenastrum* all had lowest growth rates in nutrient adjusted filtrate from *Chlamydomonas*. *Scenedesmus* had its lowest growth rate in filtrate from *Ankistrodesmus*. All species exhibited their highest growth rates in filtrate from *Selenastrum* (Table 4).

Experiment 5 - Water column mixing

In continuous mixed systems, *Selenastrum* out-competed all species (Table 3). By day 40, *Selenastrum* attained densities of up to 1.4×10^7 cells/mL in all replicates, always exceeding 4×10^6 cells/mL. In contrast, all other species averaged densities of less

than $3x10^5$ cells/mL and never attained densities of $1x10^6$ cells/mL. *Selenastrum* clearly outcompeted all other species in this experiment.

Experiment 6 - Continuous flow

In the control, (simultaneous species inoculation), three of the species, *Chlamydomonas*, *Selenastrum*, and *Ankistrodesmus*, had positive mean growth rates between day 0 and day 5, while the density of *Scenedesmus* fell below 10^2 cells/mL (Figure 1). *Selenastrum* and *Ankistrodesmus* continued to increase their densities and where co-dominants up to day 35. *Chlamydomonas* maintained population densities between 10^4 to 10^5 cells/mL until day 30 when it crashed. *Chlamydomonas* population densities rebounded between days 35 and 46 and replaced *Ankistrodesmus* as co-dominant with *Selenastrum*. After day 46, *Scenedesmus* became the dominant species. All 4 species had densities greater than an order of magnitude above their inoculation density by the end of the experiment on day 63.

In the first treatment, *Chlamydomonas* was introduced on day 0. It grew slightly from day 0 to day 5 and then crashed to less than 100 cells/mL between day 5 and day 10. This occurred even though it was the only species present during this period (Figure 2). *Chlamydomonas* population densities recovered after day 10, eventually exceeding 10^6 cells/mL by day 46. In fact, *Chlamydomonas* had recovered by day 15 so that it was the dominant species from day 15 until 51. *Selenastrum* was inoculated on day 10 after which

its population densities decreased to approximately 10^3 cells/mL until day 30. From day 30 on, *Selenastrum* population densities increased to greater than 10^6 cells/mL. *Ankistrodesmus* was inoculated on day 20 and its population densities increased slowly until day 51, after which the densities declined reached the lowest density of the four species at the end of the experiment. After invading on day 30, *Scenedesmus* grew rapidly and eventually became the co-dominant species by day 51 with *Chlamydomonas*. During the period from day 56 to day 63, *Scenedesmus* dominated, while *Selenastrum* replaced *Chlamydomonas* as it declined.

Ankistrodesmus was the first species to be inoculated into the second treatment. It remained the dominant species until day 35 (Figure 3). *Ankistrodesmus* had the lowest density at the end of the experiment in both treatments. *Scenedesmus* was inoculated second on day 10 and its population exhibited oscillations until day 46 when it became co-dominant with *Chlamydomonas* (inoculated on day 20) and *Selenastrum* (inoculated on day 30). These three species *Scenedesmus*, *Chlamydomonas*, and *Selenastrum* remained co-dominant until the end of the experiment. Both *Scenedesmus* and *Chlamydomonas* declined to less than 10^2 cells/mL immediately after being inoculated. The decline of *Chlamydomonas* may have been caused by the accumulation of secondary metabolites in the medium. Several studies have demonstrated that metabolites which accumulate during population increase can inhibit growth of the same or other species (Nalewajko and Schindler 1976; Kroes 1971; and Huntsman and Barber 1975).

Total nitrogen (nitrate-nitrite + ammonium) and soluble reactive phosphorus levels did not appear to differ between treatments. Total nitrogen levels dropped almost immediately from the daily input level of 6050 μg/L to less than 20 μg/L by day 10. From there, the levels rose slowly, but gradually until day 51 when the average for all treatments was greater than 150 μg/L. Total nitrogen levels stayed above this value for the rest of the experiment. Phosphorus levels, starting from an initial input level of 1558 μg /L, remained fairly high constant averaging around 800 μg/L until day 35, when they dropped for treatment 1 averaging less than 500 μg/L and treatment 2 averaging less than 750 μg/L, but not changing for the control. After day 35, the values for both the treatments and the control decreased to average less than 400 μg/L. Thus, phosphorus levels were always greater than nitrogen levels, so that phosphorus limitation appeared to be abated in each of the treatments (Figures 4-6).

Discussion

Classical competition experiments are usually done without regard to assembly history. This disregards one important aspect of competition which is the ability of species to alter the environment. Species differential ability to uptake and storage nutrients may lead to nutrient limitation. In addition, allelopathic compounds may be produced under favorable conditions to limit invasion success of later arriving species.

These and other effects led to "forbidden combinations" (Diamond 1975), inhibition (Connell and Slayter 1977), and "home field advantage" (Pimm 1989).

Variation in nutrient concentrations is one well documented aspect of all natural system on some time scale. Phytoplankton dynamics in natural systems are mostly controlled by seasonal differences in temperature and light. The four species used in these experiments are all green algae and what we attempted to simulate was within season dynamics. What factors may influence species dominance patterns within seasonal patterns and may lead to increased diversity? Classical competition theory predicts one species will dominate for each limiting resource (Tilman 1977, 1982). However, dominance can vary when interactions among resources occurs. Therefore, in systems which variation in resource levels and assembly processes, attempting to develop a compeititive hierarchy must take into account their dynamical nature. Thus one must realize that intransitive competitive interactions are the norm in assembling systems.

Intransitive competitive dynamics, in which dominance outcomes between competitors contain loops such that *species A* outcompetes *species B* which outcompetes *species C* which outcompetes *species A*, are known to occur between species of many phyla (Park 1954; Harper 1961; Gilpin and Case 1976; Gilpin et al. 1986). Intransitive dynamics can be a direct result of historical effects, including changes in invasion sequence and timing (Robinson and Dickerson 1987; Dickerson and Robinson 1985b; Drake 1990b, 1991; Drake et al. 1993; Harper 1961), environmental heterogeneity (Park 1954), and multiple limiting resources (Hecky and Kilham 1973). Further, as I have

shown here, the poorest competitor under one set of conditions can be the dominant species under other conditions. Because there is no logical primacy for the exclusive operation of one set of conditions across space and time, the dynamics observed here must be integrated into any general theory of organization at the community level (Grover and Lawton 1994; Drake et al. 1994).

Given that differences in invasion history can translate directly into differences in community composition, the occurrence of any particular community state is a result of the development of particular assembly trajectories. How then does one reconcile the highly deterministic outcomes observed in some studies with the kind of assembly driven variation seen here (cf. Grover and Lawton 1994; Drake et al. 1994)?

Classical competition theory reasons that the species with the greatest RUE for the most limiting resource will displace its competitors. Elegant experimental demonstrations of such dynamics have brought both mechanism and understanding to critical ecological processes (Tilman 1977; Grover 1988). I suggest that the dynamics observed in such systems must be integrated within the broader context of assembly. For example, among the four species used in this study, it was found that *Selenastrum* had the highest phosphorus RUE of all four species. However, despite a priori prediction based exclusively on RUE, *Selenastrum* was only dominant when it invaded first.

I suggest that the intransitive nature of competition observed here is the result of historical processes which function as switches, in effect turning ecological processes on and off (see also Barkai and McQuaid 1988). It is not meant that these processes simply

cease to influence community structure, instead the relative importance of controlling processes varies (Barkai and McQuaid 1988). The dominance relationships suggested by the phosphorus RUE hierarchy were easily altered by manipulating the assembly history (in both static and continuous-flow systems). For example, the effect of invasion sequence on competitive outcomes depended on the timing of inoculation events (Table 2). This makes sense because an invader needs some period of time to adjust before its effect on the community becomes evident (Crawley 1989 and Experiment 6). Under static conditions with differing invasion sequences and timing (Experiment 2), when species invaded assemblages at ten day intervals, the resulting assemblages were usually indistinguishable from those constructed by the simultaneous addition of species. Ten days represents at most three generations, thus sequence effects are muted given this invasion regime. *Scenedesmus* became the dominant species without regard to invasion sequence. This result occurred even in cases where competing species had attained densities of 2 orders of magnitude greater than *Scenedesmus* (e.g., 10^6 versus 10^4 cells/mL) prior to *Scenedesmus* inoculation.

When the period of time between invasions was increased from 10 days to 15 days under static conditions (Experiment 2) numerous outcomes became possible. When *Scenedesmus* invaded first it outcompeted all other species. However, if either *Selenastrum* or *Ankistrodesmus* colonized before *Scenedesmus* they became dominant. Only *Chlamydomonas* was unable to become dominant when it was introduced first. Thus, in the fifteen day static invasion sequences, three alternative end points were

reached depending on species inoculation sequence. This contrasts with the results of the 10 day static invasion sequence and the simultaneous invasion treatments, in which *Scenedesmus* became dominant for all sequences (see Table 3). However, when inoculation densities were increased, all species (including *Chlamydomonas*) dominated when they were introduced first in the 15 day interval treatments. Thus, any of these species given enough time and a great enough initial density can overcome any short term competitive weakness based on interaction between species.

Altering the microcosms by using filtrate medium (Experiment 4) or through continuous mixing of the water column (Experiment 5) also led to alternative competitive outcomes. For example, when filtrates media were used (Experiment 4) and the invasion interval was 15 days, the first species inoculated always dominated, however in the 10 day interval treatment, *Chlamydomonas* was always the dominant. Furthermore, when the stirring or mixing regime was changed from once a day as in Experiment 2 to continuous mixing (Experiment 5), *Selenastrum* was always the dominant species. This result negated the invasion sequence effect in Experiment 2, where *Scenedesmus* always won when the interval between invasions was 10 days.

Considerable temporal variation in population densities and species dominance was observed during the course of Experiment 6. Variation among replicates was generally low during early and late phases, however due to time lags the variation in mid phases was high in some cases. Dominance patterns at the end of these runs was fairly clear. These patterns further support the predictions that even under similar conditions of

invasion sequence and timing variablility occurs and that the dynamical nature of assembly must be incorporated into community theory.

Conclusions

Here I found that a hierarchy was easy to produce based upon phosphorus utilization efficiencies in the absence of any historical effects (Experiment 1). However, it was easy to modify the dominance hierarchy by altering assembly scenarios. Thus, rather than a single deterministic hierarchy, numerous hierarchies are simultaneously possible given variation in species colonization events, subsequent patterns of recruitment, nutrient levels, allelopathy, and the relative abundance of species encountered by an invader. Such factors serve as "switches" directing competitive outcomes. It was shown that intransitive dynamics can be produced among species which exhibit transitive competitive relationships (Keddy and Shipley 1989). The order of species dominance in competitive relationships can be altered as ecological processes are turned on and off as a system assembles. These results show that diversity can be enhanced if; (1) the context (e.g. timing of invasions) under which competitive interactions occur varies locally (i.e. spatial or temporal heterogeneity); or (2) the frequency of contextual (i.e. nutrient input or mixing) shifts is rapid enough to prevent competitive exclusion; or (3) if species have alternative life history strategies.

The third point is demonstrated by the different growth strategies of *Chlamydomonas* and *Scenedesmus*. *Chlamydomonas* grows rapidly, depleting resources quickly (see Experiment 1). This excess population may act to increase dispersal rates in open systems. *Scenedesmus*, on the other hand, grows slowly, efficiently utilize its resources so that its population can be maintained for longer periods of time and can eventually dominate numerically. This demonstrates that information gained with reductionistic strategies cannot always be directly extrapolated to community dynamics.

Finally, this study demonstrates that deterministic processes can produce a variety of patterns which look very much like those expected at random. Without information about the sequence and relative abundances of invasion events it would have been impossible to deduce the underlying mechanisms for patterns found here. This conclusion may very well explain why it has been difficult to implicate common organizational factors among similar ecological systems, or construct a cohesive framework around those systems. Obtaining information about the relative contributions of historical events (e.g. invasion sequence, timing, disturbance) to the development of variation in structure may very well hold the key to a richer understanding of ecological systems.

CHAPTER 3

Invasion Success and Community Resistance in Single and Multiple Species Invasion Models

Introduction

Ecological communities assemble through the sequential invasion (colonization) and deletion (local extinction) of species (MacArthur and Wilson 1963, 1967; Simberloff and Wilson 1969; Diamond 1975; Dickerson and Robinson 1985a). The sequence and timing of species colonization attempts, whether successful or not, may lead either to recurrent turnover in species composition (nonequilibrial dynamics) or to invasion resistant states (equilibrial dynamics) (Robinson and Dickerson 1984, 1987; Hengeveld 1986; Drake 1991). What factors determine whether a community attains a stable, invasion resistant state or experiences continual changes in species composition? Elton (1958) predicted that communities develop increasing invasion resistance as their food web structures become more tightly connected. This prediction has recently received support from the results of community assembly models and has formed the basis of a new theory of biological invasions (Hengeveld 1986; Case 1990, 1991).

While, much of the theoretical work suggests that communities do develop complete invasion resistance, recent field work to test this concept have implied otherwise (Osman 1978; Carlton 1987, 1989; Nichols et al. 1993; Hewitt 1993; Robinson et al. 1995). Elton's (1958) original prediction did not restrict the definition of invasion resistance to mean no turnover, but intended the concept as a description of the food web structure of the community acting as a filter limiting entry. He instead proposed that

some communities would be more closed to invaders while others were more "open" and would exhibit higher rates of colonization and extinction.

A number of recent studies have used assembly models in which species are allowed to sequentially attempt to invade as a community develops. Most of these model systems use dynamics of the form dN/dt=AN, where A is the community matrix matrix produced with the species interaction terms of Lotka-Volterra equations (a_{ij}) and N is the population vector. Drake (1990b) and Hewitt et al. (in press) found that complete invasion resistant states can be attained when a finite species pool is used. A number of assumptions are built into the Drake and Hewitt et al. models: a) the species source pool is limited and finite; b) single species attempted to invade each time step; c) invasion density is arbitarily low relative to Lotka-Volterra equilibrium densities; and d) Lotka-Volterra dynamics and eigenvalue analyses are used to test for community stability.

This class of models has lent sufficient support to the Eltonian concept of invasion resistance to raise it to the level of paradigm. Yet the model assumptions have never been rigorously evaluated relative to concepts of biological invasions. Since the models have played such a pivotal role in the development of a theory of biological invasions, I explicitly test several assumptions of these models while using similar dynamics and stability analyses. The objective therefore, was to test whether independently relaxing two of the assumptions, single colonizers and low density of colonizers (b and c from above), of previous Lotka-Volterra assembly models (Drake 1990b; Hewitt et al. in press) would modify the development of complete invasion resistance found in the previous studies.

I employed three simulation scenarios, to test the effect of relaxing the two assumptions. In the control simulations, all assumptions were maintained, while in some simulations two species were allowed to attempt to colonize each time step and in others I

removed the criteria to determine if species could increase when rare (relaxing the assumption of low invasion density). Both assumptions are largely derived from island biogeography theory, specifically drawn from isolated systems (MacArthur and Wilson 1963, 1967). These systems are sufficiently distant from mainland species source pools so that species arrivals are rare and generally in low numbers, but the majority of systems do not have the characteristics of isolated islands. While previous studies have used single species invasions, this assumption appears to have been motivated more by mathematical tractability rather than biological reality. Multiple invaders have been demonstrated to arrive simultaneously and at high densities in a number of studies of natural systems (Simberloff and Wilson 1969; Osman 1978; Carlton 1987, 1989; Carlton and Geller 1993; Hewitt 1993). The effects of relaxing these two fundamental assumptions of the previous Lotka-Volterra equation based models has not been reported in the literature and yet may have many consequences for invasion theory and community level theory as a whole.

Methods

Community Matrix and Lotka-Volterra Equations

The basic assembly algorithm used in this model incorporates a community matrix focusing on population growth rates, intra- and interspecific interactions terms, and food web dynamics (Drake, 1990). Population growth, intraspecific competition, and interspecific interactions are simulated using a matrix of Lotka-Volterra equations. This

leads to the time derivative of the *i*th species given by:

$$\dot{N}_i = N_i(b_i + \sum_{i=1}^{n} a_{ij}N_j), \quad i,j=1,2,3,...,n, \qquad \text{(equation 1)}$$

where N_i is the is the abundance of *i*th species, b_i is the per capita rate of increase of the *i*th species, a_{ij} is the per capita effect of species *j* on species *i*, and *n*, the number of species, which changes during assembly.

Values of *b* were randomly chosen from an uniform distribution over the intervals [$0<b_i<1$] for producers and [$-1<b_i<0$] for consumers. Values of a_{ij} were chosen from a uniform distribution over the intervals [$0<a_{ij}<1$] for the effect of a prey species on its predator and [$-1<a_{ij}<0$] for the effect of a predator on its prey. There is no direct competition between species, however, there is intraspecific competition among producers [$-1<a_{ii}<0$].

Dynamics of the system as species attempted to colonize and/or were extirpated were tracked by eigenvalue analysis of local (Lyapunov) stability of the community matrix about the equilibrium point of equation 1. This involved the examination of eigenvalues of the community matrix with elements of $a_{ij}\tilde{N}_j$. While this type of analysis was been criticized as overly simple, linearized differential equations are adequate for analysis of systems near equilibrium (see Robinson and Valentine 1979; Post and Pimm 1983). Also, the use of integration rather than eigenvalue techniques for stability analyses has been suggested, however I feel that either method will be a simplification of real systems. Eigenvalue stability analyses may result in unfeasible equilibria and this point has been widely criticized in the literature (Case, 1991; Morton *et al.*, in press). Yet these models have been successfully used to demonstrate general patterns in large multi-species systems (Robinson and Valentine 1979; Tregonning and Roberts 1979; Post and Pimm 1983; Yodzis 1989; Drake 1990b; Nee 1990). The Lotka-Volterra equations

are meant to be generalized and time averaged where the rate of reproduction and interaction terms are constant. Thus, any criticism of the use of eigenvalues should be taken in this light. I am not concerned with the specifics of the dynamics between equilbria, but instead with the fact that the equilibria do exist and are stable. Because community dynamics are very complex when more than two species are involved and my system of 60 species potentially involve interactions such as apparent competition and predator-mediated coexistence in any given time step, I believe that the best method for analysis would be the simplest. Additionally, a primary focus of this study is to directly compare these results with the previous models used in support of current invasion theory.

A regional species pool with explicit trophic interactions was constructed consisting of 60 species, with 20 producers, 20 primary consumers, and 20 secondary consumers. The number of links between each pair of trophic levels was set at 180 (for a total of 360) to give a connectance value of 0.10 ($360/60^2$). This level of connectance has been demonstrated to create communities of greater diversity than higher or lower levels of connectance (in prep). Links between predator and prey species and the total number of links for each species were randomly assigned. The links were reciprocal, in that if species *i* affected species *j*, species *j* affected species *i*.

The Assembly Algorithm

The assembly model or algorithm used herein generally follows that of previous studies (Post and Pimm 1983; Drake 1990b, 1991) with a few exceptions (Figure 7). A species pool is created with parameter values chosen as described above. Two producers are randomly selected to form the base web and then invasion attempts are made during

each time step. The effect of the number of species attempting to colonize simultaneously was examined by using either one or two potential colonizers per time step. Potential colonizers were randomly selected from the available pool which included only those species not already present in the extant community.

To test for the effect of inoculation density, potential invaders either colonized at arbitrarily low densities or at densities near their eventual Lotka-Volterra equilibria. Each species that attempted to invade when rare was added to the community matrix and evaluated for the ability to increase when rare by examining the eigenvalue of the colonizing species. If an invading species has a positive eigenvalue, then it can increase when rare and is added to the matrix. For the two species scenarios, each species were tested concurrently for the ability to grow when rare so that they would possibly interact even though both were initially rare. This then tested for the effect of simultaneous multiple invading species.

Next, if an invader is capable of increasing when rare or if this step was omitted, the augmented community was analyzed by using eigenvalue analysis. Species with a positive eigenvalue can successfully be maintained in the community. If any species had negative eigenvalues, the species with the most negative eigenvalue was deleted from the community matrix and extirpated from the community (following methodology of Tregonning and Roberts 1979; Drake 1990b; Hewitt et al. in press). Then, an eigenvalue analysis was performed on the remaining community. This was repeated until all remaining species had non-negative eigenvalues (Figure 7). Thus, one of four outcomes may occur following each invasion event: a) the invasion fails with no change in species composition; b) the invasion fails, but one or more species is driven extinct; c) the invasion succeeds and one or more species is driven extinct; or d), the invasion succeeds for one or both species (depending on the scenario) augmenting species richness. It is

important to remember that I are using this methodology to compare the effects of increasing either the number of individuals or number of species on community assembly dynamics with that of earlier papers that used the same methodology, but allowed only single invasions at low densities.

Invasion Scenarios

Twenty communities were simulated under each of three scenarios for 500 time steps. Specifically, the scenarios used were: A) single invaders at low inoculation densities; B) two invaders at low inoculation densities; and C) single invaders at inoculation densities near equilibrium. Additionally, two communities were allowed to run for 10,000 time steps for scenarios B and C. This was done to insure that fixation did not occur under these scenarios even over longer time frames.

Results

All twenty communities assembled with a single species attempting to invade per time step at low density (scenario A; Figure 7) reached an invasion resistant state (Figure 8). These invasion resistant states differed in diversity and species composition, thus multiple equilibria were found. The results of Drake (1990b) were found to be supported by this scenario even though a different species pool with fewer species and trophic levels was used. Time to invasion resistance was found to range between 16 and 337 time steps ($\mathbf{x}$ = 149.8 and s. d. = 117.97).

The communities assembled from two invaders per time step (scenario B; Figure 7) did not lead to a complete invasion resistant state after 500 or 10,000 time steps

(Figure 9). Each community assembled under scenario B followed different trajectories of changing species composition due to differences in invasion sequence.

In the twenty communities assembled under scenario C (Figure 7), where single species invaded at inoculation densities near their equilibrium values, complete invasion resistance was not attained after 500 time steps (Figure 10). This held true even when the number of time steps was increased to 10,000. Each community assembled under this scenario followed different trajectories of changing species composition and oscillating diversity as a result of random invasion sequences (see Figure 10).

Colonization success differences between scenarios were examined using Student's *t*-test. In scenario A, colonization success decreased over time as the number of successful colonizations went to zero after reaching an invasion resistant state. The probability of colonization success prior to the achievement of invasion resistance in this scenario varied greatly, ranging from 4.1 to 50.0% ($\mathbf{x}$ = 25.6, s.d. = 14.9) with decreasing success as the number of invasion attempts increased prior to reaching an invasion resistant state. However, the overall colonization success rate (over all 500 time steps) ranged from 1.6 to 11.8% ($\mathbf{x}$ = 2.5, s.d. = 1.7). In scenario B, the per species colonization success did not greatly vary over the first 500 time steps ranging from 19.1 to 30.0% ($\mathbf{x}$ = 23.5, s.d. = 2.3). Colonization success in scenario C ranged from 43.0 to 59.0% ($\mathbf{x}$ = 52.8, s.d. = 3.6) and did not exhibit any temporal trend. Thus at low inoculation density, invasion success is not significantly different ($t_{[19]}$ = 0.62; $p>.05$) when two species invade rather than one prior to attaining an invasion resistant state (in scenario A). Overall invasion success however, was significantly different between the two scenarios ($t_{[19]}$ = 32.84; $p<.001$) because of the development of invasion resistance in scenario A. Additionally, colonization success was significantly higher when the assumption of invasion at low density was relaxed (scenario C) both for comparison with the pre-

invasion resistant state ($t_{[19]}$ = 7.94; p<.001) and overall success rate ($t_{[19]}$ = 56.50; p<.001) in scenario A. Per species colonization success is significantly higher in scenario C than in scenario B ($t_{[19]}$ = 30.67; p<.001). However the total number of successful invasions was not significantly different between the two scenarios.

The development of alternative states and trajectories occurred under all scenarios. This agrees with the results found in both theoretical (Drake 1990b; Hewitt et al. in press) and empirical (Alford and Wilbur 1985; Barkai and McQuaid 1988; Drake 1991; Drake et al. 1993) studies. But only in scenario A were complete invasion resistant states attained.

These results demonstrate that in this model the relaxation of the assumption of single invading species (scenario B) leads to communities which are increasingly susceptible to invasion (19% - 30% successful attempts), but are not completely open. When the assumption of low invasion densities is relaxed this value increases to between 50% - 60% successful attempts. Thus, the communities continue to act as filters for membership. These values are similar to the results found in many studies of biological introductions in which 38% to 65% of established colonists in the recipient community succeed in establishing feral populations (Williamson and Brown 1986; Crawley 1987; Weeda 1987). Below, I discuss the implications of partial invasion resistance with respect to invasion theory.

Discussion

Current invasion theory evolved out of the earlier theories of stability and the "balance of nature" paradigm (Hengeveld 1986). Elton (1958) conceptualized the theory of biological invasions by making two central predictions concerning the invasibility of

communities. First, he predicted that invasibility will decrease as communities form highly structured food webs. And secondly, Elton (1958) stated that some communities would remain "open" readily invaded, but also susceptible to high extinction rates. From these predictions, two opposing camps have developed concerning biological invasions. One camp believes that invasion success depends on the community structure and availability of vacant niche space (Crawley 1987; Herbold and Moyle 1986). The other camp states that species attributes are the driving force behind invasion success (Pimm 1989; Safriel and Ritte 1980). I steer clear of these two extremes by stating that invasion success is influenced by both. What I are concerned with is whether the frequency and density of invaders affects the success or failure of biological invasions.

One caution with these results however, is that the total number of invading individuals increased with the number of species invading at low densities. However, the difference between the number of individuals invading at low density versus the number of individuals at near equilibrium densities for the same number of invading species is much greater that the increase in the number of individuals due to an increase in the number of invading species at similar inoculation levels.

To test the effect of increasing the densities of and/or number of invading species, I utilized a Lotka-Volterra assembly model similar to those used in past studies which have aided the development of the new theory of biological invasions (Groves and Burdon 1986; MacDonald et al. 1986; Mooney and Drake 1986; Joenje et al. 1987; Drake et al. 1989; diCastri et al. 1990). The major problem with this new theory is that it is based on a misconstrued reading of Elton (1958) and the inevitable development of opposing paradigms in science. The new invasion theory assumes that invasion resistance is either complete or entirely lacking (Hengeveld 1986).

Previous assembly models have examined the influence of single invaders under different conditions and species pool size. Given a finite species pool, Drake (1990b) demonstrated the development of invasion resistant states. When an infinite species pool is used the development of invasion resistant states is no longer attained in some models (Post and Pimm 1983; Ginzburg et al. 1988; Case 1990, 1991). Instead successful species invasions continue to occur, but the rate of success decreases with increasing community size similar to Elton's (1958) original hypothesis. Case (1990, 1991) found however, that in some cases less diverse communities did have greater invasion resistance.

In addition to theoretical models, a growing number of field studies have been used to develop the new invasion theory. While several field studies have demonstrated invasion resistance to specific taxa (Fox 1983; Burns and Sauer 1992), this does not imply resistance to all species (Simberloff 1981, 1986; diCastri 1990; Lodge 1993). None of the previous theoretical results appear to match the findings of field studies. Neither complete invasion resistance (Wilson 1961, 1969; Sutherland 1974, 1981; Sutherland and Karlson 1977; Case and Bolger 1991; Hewitt 1993) nor a continuous increase in species richness in a given patch (Odum 1969; Perino and Risser 1972; Keough and Butler 1983; Hewitt 1993) are found to occur. Thus, Elton's (1958) suggestion that invasion resistance would not be complete, but would develop as communities become highly structured food webs is supported by observation. Further, Paine (1966) and others (Sale 1977, 1978; Connell, 1979; Paine and Levin 1981; Roughgarden 1989) have demonstrated that Elton's prediction of some systems being more "open" in terms of colonization with extinction occurring frequently is correct.

The implications of the increased success of invaders as the numbers of species invading and their inoculation abundances increase are great. Introduced species such as

the gypsy moth, zebra mussel, saltcedar, and various brome grasses, appear to be able to drastically alter the environment of many natural systems (*e.g.*, Moulton and Pimm 1986; Vitousek et al. 1987; diCastri 1989; Drake et al. 1989; Mooney and Drake 1986; Nichols et al. 1990; Witteman 1992; Nalepa and Schloesser 1993). With increasing invasion success due to the factors discussed above (increased numbers and inoculation densities of species) the potential for novel "pests" is great (Carlton 1992). Thus massive biological introductions may have already had great impacts on a variety of ecological systems (*e.g.*, Groves and Burdon 1986; MacDonald et al. 1986; Moulton and Pimm 1986; Nichols et al. 1993). For example, human-mediated transport and invasion of species in marine communities has generally involved the movement of entire assemblages (Carlton 1979, 1985, 1987, 1989; Carlton and Geller 1993; Hewitt 1993). These types of movements have included oyster culture transfers, wooden ship hullfouling, and ballast water release.

The differential success of invasions due to differing numbers of colonizers and their invasion densities may explain some of the contradictions in dynamics between island (isolated) systems and mainland systems. More isolated systems experience lower frequencies of invasion attempts and similarly lower inoculation densities. I believe that increasing the frequency of invasion attempts may drive systems away from invasion resistant states and species turnover may increase due to the interaction of suites of species (extant versus invaders). This has been found to occur on Hawaiian Islands were non-native birds occupy habitat in which non-native plants dominate while native birds occupy native habitat (Witteman 1992). Thus, as disturbance causes the loss of native plants, native bird species are driven extinct. Additionally, increasing the numbers of individuals may overcome several problems concerning genetic inbreeding, population variability, and stochastic catastrophe.

While many differences between island and mainland systems have been noted, community theories are largely based on the patterns observed in isolated island systems (Diamond 1975; Brown 1971; MacArthur and Wilson 1967). I suggest that differences between these two types of systems in terms of invasion resistance may be due to the relative rates and densities of invaders.

Conclusions

In this chapter, I have shown that invasion resistance in a Lotka-Volterra community assembly model appears to be a result of unique conditions: single invaders at low inoculation densities. These conditions create patterns that are similar to more isolated island systems that have been relatively undisturbed by human activity. Multiple invaders or invasion at high inoculation densities leads to continuous turnover in species composition similar to long-term successional patterns (Odum 1969; Paine and Levin 1981) and taxon cycling (Wilson 1961) observed in many field systems. My results suggest that invasion resistance is a matter of degree, varying between complete resistance in insular systems with low invasion densities to partial resistance in local communities with high invader densities (in terms of numbers of species and numbers of individuals). Thus as human activities and transport mechanisms continue to reduce the isolation of regional biotas from one another, the numbers of species and inoculation densities of invaders will increase and result in higher susceptibilities to invasion in recipient regions and communities. In other work, I (in prep) suggest that these higher rates of invasion will not lead to higher diversity as suggested by Post and Pimm (1983), but result in increased rates of extinction and may actually lower diversity. I believe that

these results call for a re-examination of current invasion theory and the need for more empirical studies of biological invasions.

CHAPTER 4

Immigration Effects on Island Biogeography in a Community Assembly Model

Introduction

The theory of species turnover via colonization and extinction is central to community ecology. MacArthur and Wilson (1963, 1967) elucidated a general theory of island biogeography in which species diversity was hypothesized to be a result of island area and proximity to and size of a pool of species available for immigration. These factors were proposed to influence the rate at which species colonizations (successful immigration events) and extinctions occur. Islands that are larger and/or nearer to species source pools (mainlands) would have greater rates of immigration than smaller and/or more distant islands. However, extinction is assumed to be a stochastic process that is not influenced by distance so that more distant islands have fewer species due to lower rates of colonization than to extinction. The island biogeography model implicitly assumes a finite species pool and both colonization and extinction events are assumed to occur infrequently so that they are effectively singular events.

Wilson (1969) pointed out that the original island biogeography theory was non-interactive. That is during the early stage of species accumulation, population densities

of most species remain low and allow for increased coexistence, hence higher diversity (see also Huston 1979). He proposed that three additional stages develop as the process of colonization and faunal buildup continues. As population densities approach the carrying capacities of the environment, competition becomes increasingly important and thus extinctions would occur at an increased rate due to exclusion: the interactive stage. This second stage results in lower community diversity than the initial, non-interactive stage (Simberloff and Wilson 1969). As colonizations continue, it was proposed that co-adapted ensembles would develop with differing fitnesses, resulting in an assortment between ensembles: the assortative stage. Over evolutionary time scales the action of natural selection was proposed to ameliorate competitive relationships resulting in higher diversity due to niche partitioning. Whether the assortative and/or the evolutionary stages result in a reduction or increase in the equilibrial diversity of the island is a point of strong contention (Osman and Whitlach 1978; Robinson 1981; Roughgarden 1989).

While numerous studies have supported the general theory of island biogeography, particularly species diversity-area relationships and the dynamic view of species turnover (see Simberloff 1974 and Brown 1986), a number of alterations have been suggested. Brown and Kodric-Brown (1977) demonstrated that the extinction curve may flatten rather than increase exponentially due to a "rescue effect", where frequent immigration to near islands may decrease apparent extinction rates. Similarly, recent work shows that species may act at scales larger than single populations, so that local membership in islands (communities) is a result of migration among interconnected

populations creating a set of spatially interacting populations such as in "classic metapopulations" (Levins 1969; Gotelli 1991; Hanski and Gilpin 1991; but see also Harrison 1994, unpublished manuscript). This concept has been extended to the community level in which species interactions within the local community may have ramifications at the metacommunity (community of communities) level (Wilson 1992).

Prior to MacArthur and Wilson's theory, Elton (1958) developed a theory concerning the invasion of plants and animals. He suggested an interactive model where communities limit membership of species as integrated food web structures develop during assembly. Elton stated that communities become increasingly more invasion resistant over time. Various field studies have lent support to this hypothesis (Robinson and Wellborn 1988; Alford and Wilbur 1985; Fox and Fox 1986; see also Simberloff 1981 and Pimm 1991). In addition, several community assembly models demonstrate that invasion resistance either increases through time (Post and Pimm 1983; Ginzberg et al. 1988; Case 1990, 1991) or becomes complete (Drake 1990b; Hewitt et al. unpublished manuscript; Huxel and Hewitt unpublished manuscript).

The previous models (island biogeography and community assembly) assume that immigration is sufficiently infrequent that it appears to occur as single species events (MacArthur and Wilson 1967; Case 1990, 1991; Drake 1990b; Morton et al. unpublished manuscript). However, in near island systems or in island-like systems, immigation events are likely to occur at high frequencies so that species are essentially arriving simultaneously (Simberloff and Wilson 1969; Brown and Kodric-Brown 1977; Osman

1978; Punttila et al. 1991; Menge 1991; Kadmon and Pulliam 1993; Hewitt 1993). Similarly, biological invasions or human-mediated introductions have been demonstrated to transport species ensembles and entire communities between non-contiguous biotic provinces (Carlton and Geller 1993, Vermeij 1989, 1991; Webb 1991; Mack 1986; Moulton and Pimm 1986). Consequently, in Chapter 3, I examined the influence of increasing either the inoculation density of single invading species (the number of individuals arriving) or the number of simultaneously invading species on the development of invasion resistance. I found that complete invasion resistance did not occur in either scenario with multiple trophic level models, despite the fact that most species were not able to successfully invade. These results suggest that the effect of multiple invading species may provide a basis for linking invasion and island biogeographic theories. Here, I examine the influence of increasing the number of invading species per time step on colonization, extinction, turnover, and stability in a simulation model of community assembly.

Methods

The Community Matrix and Lotka-Volterra Equations

The basic model used in this chapter is the same as that used in the previous chapter. The same values for the growth terms and interaction terms were used, as were

the number of species in each trophic level and the number of links. The only difference was in the assembly scenarios that were examined.

Assembly Scenarios

Ten communities were simulated for each level of immigration. The number of species immigrating was either fixed at two, three, four, five, eight, or ten species or the number varied and was randomly drawn from a uniform distribution over the range from one to ten, inclusive, each time step. Herein, increasing immigration means an increase in the number of species invading in any time step and consequently, the total number of individuals invading increases as the number of invading indidviduals per species is constant. Again, each simulation was run for a total of 500 invasion/time steps.

Statistical Analyses

Analyses were performed separately for the fixed number of immigrating species (I=2,3,4,5,8,10) and for the variable number of immigrating species (I=1 to 10). For both, ANOVA analyses were performed to test for significant differences in measurements of colonization, extinction, and turnover versus number of immigrating species. *A posteriori* tests were conducted for significant ANOVA's using the T-method which allows multiple pair-wise comparisons corrected by the Bonferroni method (Sokal and Rohlf 1981).

Diversity-Stability Analyses

To test for of a dynamic equilibrium of species diversity as assumed by the island biogeography model, I utilized the concept of stochastic boundedness (*sensu* Chesson 1978). This concept is used to demonstrate whether relatively small fluctuations around the mean are within the 95% confidence band for a hypothesized normal distribution (see Keough and Butler 1983; Kay and Butler 1983). This assumes that there exists an upper and lower bound that is exceeded with the probability of $(1-\varepsilon)$ and the width of the $(1-\varepsilon)$ confidence band defined by those bounds is $\leq 2\omega \mathbf{S}$. Where the 95% confidence interval $\varepsilon = 0.025$, **S** is the mean of S (here species richness) and ω is an arbitrary constant which defines the "smallness" of the fluctuations. The value of ω has been suggested to be 0.2 for "narrow" boundedness (Keough and Butler 1983; Kay and Butler 1983), but Osman and Dean (1987) surveyed reported equilibrium systems and found that this is too restrictive for systems in which the average species richness is less than 10 and instead recommend using $\omega = 0.3$. Herein I follow the relaxed definition (Osman and Dean 1987) and use $\omega = 0.3$. To determine whether species richness varies oveer time more than can be expected, I utilize a *t*-test based upon the coefficient of variation and the standard error of the sample statistic, S (see Keough and Butler 1983; Kay and Butler 1983).

Results

To better present the results, I have broken the results into two sections: fixed (2, 3, 4, 5, 8, 10) or variable (1 to 10 randomly selected) immigration scenarios.

Fixed number of immigrants

Colonization, extinction, and turnover dynamics were all strongly influenced by the level of immigrant species per time step. The rate of colonizations, measured as the number of successful colonizations per time step, significantly differed between the level of immigrants ($F_{5,54}$=272.3, P<0.001) (Table 5). Using the T-method, mean colonization rate increases with increasing number of immigrant species and significant differences were found for all pairwise comparisons (P<0.05) (Table 5).

Colonization probability, measured as the percentage of successful colonizations per immigration attempt (time steps times number of immigrants per time step), differed significantly with the level of immigrants ($F_{5,54}$=9.63, P<0.001) (Table 5). T-method tests showed significant differences only between the level of two immigrant species and the other levels of immigrants (P<0.05) (Table 5) with a sharp drop in colonization probability for immigration attempts involving more than two species.

The rate of species extinctions, here measured as the number of species extinctions per time step, also differed significantly with the level of immigrants ($F_{5,54}$ =272.5, P<0.001) (Table 5). T-method demonstrates that significant increases in extinction rates were found with increasing level of immigrants for all pairwise comparisons (P<0.05) (Table 5).

Turnover rate, measured as the number of colonizations plus the number of species extinctions divided by two, also differed significantly with the level of immigrants ($F_{5,54}$=272.9, P<0.001) (Table 5). Using the a posteriori T-method, increases in turnover rate were found with increasing level of immigrants and significant differences were found for all pairwise comparisons (P<0.05) (Table 5). Note that the

most prevalent net turnover was zero (from 46.7% at the level of two immigrants to 24.6% at the level of ten immigrants) (Figure 11).

Significant differences in average diversity were found between levels of immigrants ($F_{5,54}$=19.3, P<0.001). Diversity increased over the range of two immigrants to a peak at five immigrants and then decreased (Table 5). T-method tests showed only that average diversities were similar for all levels greater than two immigrants, but these differed significantly with two immigrants (P<0.05). This was due to the number of both colonizations and extinctions increasing as the immigration level increased so that there was no significant difference in net turnover, measured as the number of colonizations minus the number of extinctions, between levels of immigration ($F_{5,54}$=0.74, P=0.598).

Using the methodology of Keough and Bulter (1983), two variables are calculated to assess stochastic boundedness: ω and a t-statistic. ω is a measure of the width of the deviation of the 95% confidence interval and *t* is the Studentized *t*-test comparing the sample variation against that predicted by the normal distribution. For *t*-test the critical value at α=0.01 is 1.798 and for ω the critical value is 0.30 (Osman and Dean 1987). I had hypothesized that if my model systems exhibited a dynamic equilibrium as predicted by island biogeography theory then they would be stochastically bounded. However, both measures far exceed the hypothesized critical levels at each level of immigrant and thus, the definition of stochastic boundedness is violated (Table 6).

Variable number of immigrants

Because there was variability in the number of occurrences of different size invasion events due to randomness of the selection of the number of immigrants, percentages were used for analyses of colonizations, extinctions, and turnover events.

This data was then transformed by arc sine of the square root of the percentage (Sokal and Rohlf 1981).

Colonization probability per time step, measured as the percentage of time steps in which successful colonization of at least one species occurred, significantly differed between levels of immigration ($F_{9,90}$=15.66, P<0.001) (Table 7). T-method tests demonstrated an increasing trend in the per time step colonization probability (P<0.05) (Table 7). This increase was rapid from one to five immigrants and leveling off for greater than four immigrants.

The colonization probability per immigrant significantly differed with the level of immigrants ($F_{9,90}$=3.64, P<0.001) (Table 7). T-method tests demonstrated a decreasing trend in the per immigrant colonization probability (P<0.05) (Table 7). There is a noticable decline in colonization success per immigrant when more than two species invaded per time step.

Extinction, measured as the percentage of invasion events that lead to loss of at least one species, differed significantly with the level of invaders ($F_{9,90}$=15.50, P<0.001) (Table 7), but reached a peak at eight invaders. *A posteriori* tests showed significant differences between levels of immigration (P<0.05) (Table 7). Extinction probability increased continuously until eight immigrants and then decreased.

The average magnitude (number of species) of extinction events significantly differed with the level of immigrants ($F_{9,90}$=7.31, P<0.001) (Table 7). T-method tests demonstrated significant differences between levels of immigration (P<0.05) (Table 7). The average dropped sharply from one immigrant to two and then evened off until the level of seven immigrants and then decreased sharply again.

The probability of species diversity to increase rose with the number of immigrating species ($F_{9,90}$=8.54, P<0.001) (Table 7). This was due mainly to low

numbers of invaders resulting in fewer, larger extinction events while increased numbers of invaders led to more smaller extinction events, while colonization success increased with number of invaders.

Turnover probability, measured as the percentage of time in which a colonization or extinction event occurred, increased as the number of species that attempted to immigrate simultaneously increased ($F_{9,90}$=48.10, P<0.001) (Table 7). A posteriori tests again show significant differences with turnover which reaching a peak at seven to nine immigrants and then decreasing (P<0.05) (Table 7).

Discussion

Results from this study demonstrate that increasing the number of simultaneously immigrating species leads to increased colonization, extinction, and turnover (Tables 5 and 7). In addition, the violation of the assumption of a dynamic equilibrium as proposed by MacArthur and Wilson (1963, 1967) occurred at each level of immigration (see Table 6). This occurs despite the fact that the per species colonization probabilities were low (less than 25%; Tables 5 and 7). Thus, the hypothesis of a dynamic equilibirum does not seem valid in trophically dynamic successional (assembling) systems.

Furthermore, immigration rates are postulated to correlate with isolation of the recipient community from a species pool. Noninsular systems (mainlands) are proposed to have higher rates of immigration, while insular systems (far islands) have low rates of immigration. Thus, these results suggest that mainlands have greater rates of colonization, extinction, and turnover. This is inconsistent with island biogeographic theory which predicts higher colonization rates for nearer islands, but no change in extinction rates with respect to isolation, leading to higher diversity for nearer islands.

Instead, I found that while diversity significantly varied across immigration rates (degree of isolation) ($P<0.001$), it reached a peak at three to five simultaneously immigrating species (Table 5). Why do these inconsistencies occur between these results and island biogeography theory? I believe that these are due to non-interactive nature of the MacArthur-Wilson model (Wilson 1969) and due to the nature of assembling systems. This inconsistency with island biogeography theory for successional systems with trophic dynamics was hinted at by MacArthur and Wilson (1967). Since the derivation of their model, a number of interactive theories and models have been developed which concern colonization. Below, I mention some these models, but focus on invasion theory and possible links with the theory of island biogeography.

Theories and models concerning colonization

Ricklefs's (1987) discussion of the role of local processes versus regional processes in structuring communities has led to much discussion concerning the relative importance of scale processes and phenomena (see Ricklefs and Schluter 1993). Regional processes affect migration and evolution, while local processes involve species interactions. Thus, the linking of the theory of island biogeography with invasion theory is essentially a linking of regional and local processes (see Holt 1993).

In general, there are a number of theories and models other than island biogeography and invasion theory which rely upon colonization rates to drive extant community diversity . These include: "supply-side" ecology (Gaines and Roughgarden 1985; Roughgarden, Gaines and Pacala 1987; Roughgarden, Gaines and Possingham 1988; Grosberg and Levitan 1992); lottery succession (Sale 1977, 1978; Fagerström

1988); source-sink models (Shmida and Wilson 1985; Holt 1985; Pulliam 1988); and Huston's general hypothesis (1979, 1994).

While, I focus on island biogeography and invasion theory to simplify the discussion, many of the arguments I use to link these apparently disparate theories are applicable to other theories and models of community development.

Island Biogeography and Invasion Theory

The limiting assumption of immigration occurring as single species events is common among the theory of island biogeography and invasion theory. Yet, numerous studies have demonstrated that immigration of species can occur simultaneously in a variety of systems (Connell 1961, 1985; Simberloff and Wilson 1969; Diamond 1973; Brown and Kodric-Brown 1977; Harper 1977; Sutherland and Karlson 1977; Osman 1978; Venerable and Lawlor 1980; Sutherland 1981; Reice, Wissmar and Naiman 1990; Beatty 1991; Kadmon and Pulliam 1991; Menge 1991; Punttila et al. 1991; Carlton and Geller 1993; Hewitt 1993; Gilpin 1994). While realizing that proximity to a species pool influences immigration, I are more concerned with systems that experience high rates of immigration such as near-shore and mainland systems.

The theory of island biogeography states that island systems have a dynamic equilibrial number of species as a result of balance between colonization and extinction rates. However, some systems violate the assumption of a dynamic equilibrium such as these model systems and other studies (Keough and Butler 1983; Abbott and Grant 1976). The incorporation of assembly dynamics as illustrated by invasion theory provides insight into these non-equilibrial dynamics.

Invasion theory must be viewed in the context of the assembly of communities, the colonization and extinction of species over time (Elton 1958). Drake (1990a) suggested that some community states could only be reached through the participation and ultimate loss of certain species during the assembly process. Odum (1969) demonstrated that successional systems undergo periods of buildup and collapse and that these cycles were necessary for long-term persistance. Thus, invasion theory must take into account the dynamic nature of assembling systems. Invasion theory as envisioned by Elton, contends with the ability of species to colonize a system that may inhibit or enhance its ability to colonize. Due to the dynamic nature of assemlbing systems, the ability of a species to colonize a particular patch changes over time with the composition of the community and its food web structure. The dynamic nature of assembling systems does not fit well with the assumption of a dynamic equilibrium of island biogeographic theory.

The theory of island biogeography concerns heterogeneous systems of multiple patches, each patch exhibiting a dynamic equilibrium of species diversity. Over the range of patches, colonization and extinction rates may be averaged resulting in lowered turnover and a regional equilibrium number of species. However, Abbott and Grant (1976) showed that even for isolated islands the assumption of a dynamic equilibrium may be violated. Diamond (1973) discusses the possible effects due to lag time of returning to an equilibrium following a perturbation or mass invasion of a group of immigrant species. Such a mass invasion may temporarily oversaturate the system with species, leading to increased extinction rates as population levels and competitive interactions both increase. Simberloff and Wilson (1969) found that the refaunation of mangrove island insect assemblages had similar diversity overshoots due to low population numbers in early phases. Huston (1979) hypothesized that high levels of

diversity of high immigration systems could only be maintained if population growth rates were low so that competition would be minimized.

Various studies have demonstrated that as diversity increases, species packing will lead to increased extinction rates as niche space narrows and/or competition increases (MacArthur 1958; Schoener 1974; Rummel and Roughgarden 1985; Roughgarden 1989; Nichols, Thompson and Schemel 1990; Case and Bolger 1991). This issue is central to the concept of a balance between colonization and extinction as predicted by the theory of island biogeography. However, the accumulation or oversaturation of species resulting in high diversity regions may be due to favorable colonization of additional species (Simberloff 1981; Crawley 1987; Stevens 1989). This results from persistent or intense rains of propagules which lead to a "rescue effect" limiting or reducing extinctions (Harper 1965; Brown and Kodric-Brown 1977). Stevens (1989) suggests this may exaggerate diversity in the tropics with the propensity of species to establish non-reproductive, peripheral populations in a source-sink situation (Holt 1985; Pulliam 1988).

Other studies have shown that the invasion of predators affects extinction directly through overconsumption and density dependent predation, or indirectly through the amelioration of competition (Paine 1966; Janzen 1970; Jefferies and Lawton 1984; Billick and Case 1994; Wooten 1994). Keystone predators are known to reduce the population levels of superior competitors, preventing the competitive exclusion of inferior species (Paine 1966, 1974) or alternatively forcing the system into novel trajectories in which competitive intransitivities may persist (Barkai and McQuaid 1988; Huxel et al. unpublished manuscript).

The attention to historical effects on community structure is linked to the reconciliation of the effects of regional and local processes (Ricklefs and Schluter 1993).

Historical effects are known to influence colonization, either through facilitation or inhibition by predecessors (priority effects), vicariant distributions of taxa, or origination (Sutherland 1974; Connell and Slatyer 1977; Sutherland and Karlson 1977; Robinson and Valentine 1979; Alford and Wilbur 1985; Drake 1990a, 1990b, 1991; Drake et al. 1993; Hayden et al. 1994; Huxel et al. unpublished manuscript). Priority effects include the exclusion of competitors by earlier colonizers, either by preventing "forbidden combinations" (Diamond 1975) or by actively outcompeting the immigrant via a "home field advantage" (Pimm 1989). Priority effects may also allow for the switching of predator and prey relationships (Barkai and McQuaid 1988). Additionally, trophic accomodation is a central requirement for the establishment of heterotrophs, which cannot survive without the presence of prey or host. Similarly, the role of mycorrhizae as a limiting factor in the colonization of many plant species has been well documented (Perry et al. 1990; Richardson et al. 1994; Perry 1995). These patterns are evident in studies of the recolonization of Rakata and Krakatau Islands which have demonstrated that all taxa examined do not show equilibrium trends due to successional (historical) effects (Thornton et al. 1993; Bush and Whittaker 1993). The effects of trophic dynamics in a successional system on the shape of colonization curves and on the island biogeography model in general are being explored (Hewitt and Huxel unpublished manuscript).

Conclusion

To test the influence of increasing the number of simultaneous immigrating species, I conducted simulations with the same community assembly model used in a previous study in which I demonstrated that the relaxation of the assumption of single

invading species resulted in the lack of complete invasion resistance (Chapter 3). Herein, I found that colonization, extinction, and turnover rates increase with an increase in the number of immigrating species. Additionally, an increase in immigrating species led to the transgression of stochastic boundedness (Table 6), despite the use of deterministic equations and equilibrium dynamics. This demonstrates that increased immigration rates may result in non-equilibrium dynamics and increased susceptibility to invasion and extinction of inhabitants. With documented increases in the rates of species immigration due to the increase of human transport activities (Carlton 1985, 1989; Carlton and Geller 1993), there is the potential for increased rates of turnover and extinction of the world's biota. Ballast water studies have demonstrated the frequent introduction of numerous species into estuarine and near-shore habitats (Carlton 1979, 1987, 1989). The successful colonization of several species has been well documented (Carlton et al. 1990; Nichols et al. 1990; Hallegraeff and Bolch 1992). While, regional diversity has increased for some of these systems (e.g. San Francisco Bay, California and Coos Bay, Oregon), local diversity has decreased in specific patches and the long-term effects are unknown (Nichols et al. 1990; Hewitt 1993). The potential for drastic change through colonization and subsequent extinction of species appears to be especially important for systems that have not previously experienced high immigration rates and have high levels of endemicy (Groves and Burton 1986; MacDonald et al. 1986; Mooney and Drake 1986; Joenje et al. 1987; Drake et al. 1989; diCastri et al. 1990; Witteman 1992; Pimm et al. 1994). Thus, as MacArthur and Wilson (1967) suggested, island biogeography equilibrium theory may not be valid for successional systems which have trophic dynamics, so that new models and theories that can incorporate both colonization and trophic dynamics are needed to address many ecological issues.

CHAPTER 5

Collapse Dynamics on an Ecological Landscape: A Model of Interacting 1/f Perturbations

Introduction

Nature is replete with systems possessing fractal properties such as apparent measured shoreline lengths (Mandelbrot 1982), light from quasars (Nolan et al. 1981; McHardy and Czerny 1987), the Belousov-Zhabotinsky chemical reaction (Roux et al. 1983), and earthquake dynamics (Hastings and Sugihara 1993; Hough 1995) (see also Milne 1992). These systems derive much of their structure from the processes of self-organization (Kauffman 1993), a kind of assembly mechanic. Self-organization occurs when pattern arises in excess of that which could be predicted based on a detailed knowledge of initial conditions. Consider for example the elegant sand-pile metaphor offered by Bak et al. (1987b). When a sand pile is assembled by the sequential addition of single sand grains, the pile grows until a critical state or *angle of repose* is reached (Bak et al. 1987, 1988; Tang and Bak 1988; Jaeger et al. 1989; Held et al. 1990; Weisenfeld et al. 1990). At the angle of repose further grain additions can induce sand-slides or collapse events. The frequency-magnitude distribution of collapses that occur following the attainment of the angle of repose is best described by a simple power-law with the exponent w assuming values between 0.98 and 1.57 (Bak et al. 1987, 1988; Tang and Bak 1988; Jaeger et al. 1989; Held et al. 1990; Weisenfeld et al. 1990; Drake et al. 1992; Kauffman 1993). The pile reaches a self-organized critical state. There is nothing about a sand grain or even in sand grains which suggest the emergent properties of the pile.

It is a natural extension to substitute entities such as species for sand grains and extinctions for collapses. Similarly, patches in the landscape may change state or collapse as a function of disturbance. The common theme among these systems is in the temporal dynamic (e.g., duration of, time between, or magnitude of collapses) which are all manifest as simple power-laws (Tang and Bak 1988; Kauffman 1993). Such trends are suggestive of basic and general rules of system assembly or construction.

In these systems the resulting distribution is assumed to be a function of a single underlying perturbation (*monofractal*). In contrast to the physical systems described above, ecological systems are subject to multiple sources of perturbation in both space and time from various sources including both biotic and abiotic factors (Pickett and White 1985; DeAngelis et al. 1986). These perturbations may differ in relative frequency of occurence and patterns of dispersion across space and time (i.e., random, random-walk, and aggregate). To extend the sand pile metaphor, consider the effect of simultaneous additions of multiple sand grains on the magnitude of sand pile collapse. While the addition of single sand grains induces a typical "$1/f$" signal , the nature of the aggregate signal which results from simultaneous additions is unknown. In such cases, the observed dynamics should result either from interactions between perturbations, *or* from spatial and temporal variance of the underlying mechanisms creating those perturbations (Steele 1985; Steele and Henderson 1994).

Herein I explore the dynamics of multiple interacting perturbations across a range of spectral coefficients on an ecological landscape. Do these interacting perturbations result in sufficient overlap to cause a deviation from a power-law distribution or is the probability of overlap too low to alter the simple multiplicative power-law relationship? I examine the relative explanatory power of the two alternative statistical distributions

(multiplicative power-law and gamma) with regard to the results from Monte Carlo simulations.

Theoretical Distributions

A power-law is simply an exponential scaling relationship between dependent and independent variables. Here, I use a power-law probability distribution of the type $(f)=1/f^{w}$, where (f) is the probability of the occurrence of a disturbance of magnitude f. The exponential scaling parameter w is defined as the slope of the relationship between frequency and magnitude of disturbances on a log-log plot. Thus, $1/f^{w}$ is a probability function over the range $f = 1$ to z, where z is the magnitude of the largest possible perturbation event. For example, in a landscape of 100 patches (e.g., 10x10 square lattice), the largest possible perturbation event would impact 100 patches or the entire landscape.

It has been offered that multiple "1/f" relationships should interact in a multiplicative fashion (West and Shlesinger 1990; Lewin 1992; Kauffman 1993). Such nonoverlapping power-law perturbations result in simple multiplicative distributions of the type:

$$p(f) = \frac{1}{f^{\omega_1}} \times \frac{1}{f^{\omega_2}} \times \cdots \frac{1}{f^{\omega_n}} \qquad \text{(equation 1).}$$

This holds when the multiple perturbations do not spatially overlap or lack independent placement on the landscape. However, when such relationships overlap in a spatio-temporal fashion (e.g. Pickett and White 1985; O'Neill et al. 1986; Turner 1987) these simple arithmetic operators do not hold. The expected size of total collapse is a result of

the sum of collapses from the individual (component) perturbations adjusted by the number of patches where overlap occurs. For example, with three perturbations the probability of a particular total collapse size is:

$$P(A,B,C) = P(A) + P(B) + P(C) - P(A \cap B) - P(A \cap C) - P(B \cap C) + P(A \cap B \cap C) \text{ (equation 2),}$$

where A, B, and C are the individual perturbations. This relationship indicates that the resulting distribution of collapse sizes (c_{total}) will exhibit two deviations from the expected multiplicative distribution: 1) a modal shift will result if the probability of a total collapse of size n (where n is the number of perturbations) is greater than the probability of overlap; and 2) there will be a decrease in the larger collapse sizes due to the increased probability of overlap with large component collapses and finite system size.

In ecological systems both spatial and temporal overlap frequently occur (Sousa 1979, 1980; Pickett and White 1985; O'Neill et al. 1986; Turner 1987). Consider my example landscape of 100 patches, if 50 patches (individuals or local populations) experience disturbance in the form of predation, they may still be subject to abiotic disturbance (e.g., a wave or log impact in marine systems, fire in terrestrial systems affecting 30 patches) which impinges upon some or all of the previously affected patches.

In contrast to the simple multiplicative property for multiple power-laws (equation 1), the generalized gamma-distribution has been effectively used to predict the behavior of multiple component systems (Crutcher et al. 1977) and exhibits many of the deviations due to overlap described above. This distribution ranges from a negative exponential to a canonical normal distribution. The gamma-distribution, given as:

$$f(x) = \kappa \exp^{\left(-\frac{x-\alpha}{\beta}\right)} \left(\frac{\left(\frac{x-\alpha}{\beta}\right) \quad +\gamma - 1}{\gamma - 1} \right)^{(\gamma-1)} \qquad \text{(equation 3)}$$

where **a** is the location parameter (mode), **b** is a scale parameter, **g** is a shape parameter, and **k** is a shape parameter (maximum frequency), has previously been used to describe exponential waiting time distributions (Crutcher 1977) for physical systems such as equipment failure (Jørgensen 1982) and rainfall events (Haggard et al. 1973).

The multiplicative power-law model can only result in power-laws of larger spectral coefficients (change in the shape of the curve) than the component distributions (equation 1). In contrast the generalized gamma describes a shift in the mode of the distribution as well as a change in the shape (the slope of the curve over the portion above the mode) consistent with that predicted by the incorporation of an overlap component into the multiplicative power-law.

Methods

A Model of Multiple Perturbations Interacting on a Landscape

To explore the interaction of signals generated by multiple perturbations, I conducted Monte Carlo simulations (10,000 iterations per scenario) using a landscape (16x16 lattice) of 256 patches or cells (Figure 12). Each patch within the landscape could be occupied by a biotic unit such as an individual, population, or community. The presence or absence of a biotic unit in any given patch is assigned a binary form where a

value of one indicates presence and a value of zero indicates absence. Beginning each iteration with a saturated landscape in which all patches were occupied, I imposed from one to ten simultaneous perturbations.

Each perturbation was assigned a collapse magnitude which was randomly selected from a specified $1/f^w$ frequency-magnitude distribution (for w=0.5, 1.0, 1.5, 2.0, and 3.0). The collapse magnitude specifies the number of patches affected during a perturbation event ranging between 1 and 256 patches. This does not necessarily assume that the perturbation follows a power-law distribution function, but that the result of the perturbation (the frequency histogram of disturbance magnitude) is power-law distributed. Two types of multiple perturbation scenarios were used: scenarios in which either 1) the spectral coefficients were identical; or 2) the spectral coefficients were disparate. In the disparate scenario, the interaction between all possible pairs was simulated. Additionally, four combinations of five perturbations were examined in which four perturbations with identical spectral coefficients (w =2 or 3) were combined with a single disparate perturbation (w=0.5 or 1.0).

The terminology used in the many *catastrophic* and *1/f* perturbation models in the literature is not standardized. In this model I use *collapse* to refer to an extinction event in a single patch, *perturbation* to refer to the mechanism or process creating patch collapse, and *disturbance* to refer to the result of a perturbation (the actual collapsed patches). Herein the dynamics of "collapses" are solely the result of perturbations imposed upon the system.

Depending upon the scale of measurement the patch can represent a range of biotic units. At the level of population dynamics each patch represents the location of an individual and thus a collapse will cause the death of individuals in all perturbed patches. In a landscape or metacommunity system where each patch is a community, a patch

collapse will cause the entire community to go extinct. Here, I will discuss the model from a landscape approach where each "patch" contains a community.

Distribution Descriptions

Frequency histograms of collapse magnitudes (total disturbance sizes) were generated for Monte Carlo simulations. This allowed single perturbations to be contrasted to the various combinations of perturbations with either identical or disparate w (see Table 8 for combinations). The resulting size-frequency histograms for randomly dispersed disturbances were analyzed for mode and skew. Partial linear regressions were performed on log-log transformed data above the mode in accordance with an assumption of multiscalar self-affinity (Sugihara and May, 1990; Hastings and Sugihara 1993). The slope or aggregate spectral coefficient of the partial linear regression, here defined as w, and the Pearson correlation coefficient (r^2) were calculated.

Placement of Collapses and Disturbance Types

Disturbances were placed on the landscape in three distinct dispersion patterns: 1) the random placement of all disturbed patches without correlation between patches (Figure 12a); 2) a random-walk from a single, randomly selected "seed site" resulting in a loosely structured set of contiguous disturbed patches (Figure 12b); and 3) an aggregated, square walk from a randomly selected "seed site", resulting in a tight clump (Figure 12c). While perturbations are independent of one another with the potential for individual patches to be affected by multiple disturbances, extinction of a particular patch can occur only once per iteration.

Placement of disturbed patches across the landscape simulates different types of external perturbation. Different types of collapses can be detected in different systems. For instance, slow burning fires occur as aggregated clumps, while fast moving fires may follow random walks, and lightning strikes can occur either randomly across landscapes or in loose aggregations dependant upon storm intensity. Thus, in my example, the impact of grazing may follow a random-walk while fire may aggregate. Here, I did not allow for the interaction of different dispersion types but assumed that all perturbations had the same dispersion patterns.

Similarly, I did not allow the presence or result of one perturbation to alter the dispersion pattern of a second. Again using the example above, the dispersion of grazing disturbance could be altered if fire had already been placed on the landscape. Thus the two perturbations would lose independence of placement, altering the potential for overlap. I assumed however, that the disturbances were placed on the landscape simultaneously maintaining their independance (Figure 13).

The histograms for varying disturbance dispersions (random, random-walk, aggregate) were compared for all combinations of interacting perturbations and component values *via* correlation analysis. Except at low w values (<1.0), the differences between dispersion patterns were not significant ($r>0.05$; Table 9). Thus for values equal to or greater than 1.0, further analyses were conducted using the values from random dispersion alone.

Curve Fitting

Random dispersion size-frequency histograms were fit to both power-law and four parameter gamma-distributions over the entire range of collapse magnitudes using

non-linear least squares correlation analysis. For these analyses only perturbations with identical spectral coefficients (for w=1.0, 2.0, and 3.0) were evaluated, however the disparate spectral coefficient scenarios were previously shown to exhibit similar patterns of distribution alterations (Table 8). The power-law aggregate spectral coefficient of the complete linear regression is here defined as W_c in contrast to W_p for the partial linear regression. This measure (W_c) acts as a direct comparison with the from the multiplicative power-law model (equation 1).

Results

Distribution Descriptions

Initially it was necessary to document the behavior of single perturbations for each value as a comparison with *n* multiple perturbations. Each of the distributions resulted in spectral coefficients (w) that closely approximated the values selected for the perturbation distributions (Table 8). Note that for w values of 2.0 and 3.0, larger magnitude collapses were very rare (Figure 14). In fact, for =3.0, the largest collapse magnitude was only 24.2% (62 patches) of the maximum.

For multiple perturbations with identical exponents and randomly dispersed disturbances, both the minimum collapse magnitude and the mode shifted to the right (Figure 14) leading to decreasing skewedness with increasing number of interacting signals (Table 8). Resulting spectral coefficients (W_p) decreased with the number of interacting perturbations for w= 0.5, 1.0 and 1.5. System boundedness, in which maximum collapse size was limited by the size of the 16X16 lattice (c_{max} = 256 patches), altered the W_p sufficiently to lead to a positive slope at 2 perturbations for w = 0.5 and 4

perturbations for =1.0 (Table 8). Multiple $1/f^{2.0}$ perturbations however, exhibit little change in W_p, while for $1/f^{3.0}$ perturbations the W_p increase as the number of perturbations increase (Table 8).

The skewedness value for multiple interacting $1/f^{1.0}$ decreases from 9.614 for one perturbation to 2.468 for five perturbations, a reduction of ~75%. While for $1/f^{3.0}$, the reduction is only ~33%, from 15.657 to 10.462. Thus, smaller component w values lead to greater changes in both skewedness and in aggregate spectral coefficient.

For multiple perturbations where component w were less than 2.0, the resulting aggregate spectral coefficients (W_p) were nearer to the lowest w value assigned to any single component perturbation. For example, when a $1/f^{0.5}$ perturbation interacted with a $1/f^{1.0}$ perturbation, the resultant spectral coefficient (W_p) was 0.185 and when it interacted with a $1/f^{3.0}$ perturbation , the coefficient was 0.530. This is compared to a single $1/f^{0.5}$ perturbation having a coefficient of 0.519. As the difference between component perturbation exponents increased, the aggregate W_p's approximated the lowest component (Table 8). In these situations however, the mode was largely determined by the number of interacting perturbations and remained the same regardless of the disparity between the component (Figure 15).

Placement of Collapses and Disturbance Types

The three disturbance dispersion types were evaluated for differences in the resulting frequency-magnitude distributions for multiple, interacting perturbations. No significant differences were detected in pairwise comparisons between dispersion types (random, random-walk and aggregated) for distributions from identical component w greater than 2.0 (Table 9). The pairwise comparisons of the distributions exhibited

significant correlations with one another ($r^2 > 0.990$) for all combinations of perturbations with s greater than 2.0. However, as the resulting W_p values decreased (due to multiple, interacting signals) the correlation between dispersion types decreased. For multiple perturbations with $w < 1.0$ the resulting distributions were not significantly different from 0 and thus were not compared between disturbance types (Figure 14, Table 9).

Curve Fitting

As previously stated, due to a lack of significant differences between disturbance dispersion types further evaluations were performed on data from randomly dispersed scenarios only. Initially the power-law correlates well with single perturbation distributions for all w ($r^2>0.900$). The mode shift and change in slope associated with increasing number of perturbations reported above (see *Distribution Descriptions*) however, result in decreasing correlations (Table 10, Figure 16). The change in r^2 between number of perturbations was found to decrease as the component perturbation increased (Table 10). In contrast, the gamma-distribution exhibits strong correlation with all multiple perturbations distributions for w=2.0 and 3.0 ($r^2>0.986$). For w =1.0, the gamma-distribution was only fit to scenarios with 2 interacting perturbations, resulting in an r^2 =0.731 (Table 10).

The aggregate spectral coefficients (W_c) exhibited rapid departure from the expected multiplicative power-law W values. For example, 4.0 is the W for two perturbations with component w of 2.0, yet the measured W_c is 1.789 (Table 10). While the multiplicative power-law predicts an additive increase in the W the actual measured W_c decreases (Table 10).

The gamma-distribution parameters **a** and **k** (the x,y coordinates of the estimated mode; Table 10) track the actual mode and frequency (Table 8). The values for **a** increase and for **k** decrease with increasing number of perturbations tracking the tendancy towards a normal distribution seen in Figure 3. While the scale parameter, **b**, increases with perturbation number the shape estimate, **g**, remains near 1.0, deviating only when the number of perturbations reached 8 or more.

Discussion

The objective of this work was to determine whether multiple interacting perturbations would lead to or deviate from a multiplicative power-law given the potential for overlap. If a deviation was detected, what type of statistical distribution would best describe the results? Since the generalized gamma-distribution has both modal and shape parameters, it was hypothesized that this distribution would adequately model the data.

I found that interacting power-law perturbations did indeed result in sufficient overlap to induce a deviation from the distribution predicted by equation 1. Additionally, the concommitant shift in the mode with increasing perturbations and the alteration of the shape of the curve showed that the gamma-distribution was a better descriptor of the resulting distribution (Figure 16).

The primary reason why the dynamics described herein are best fit to a gamma distribution is that the low probability of overlap at small perturbation collapse sizes induces a modal shift. Similarly, the increasing probability of overlap with increasing component disturbances alters the shape of the curve (equation 2). Thus, perturbations

interact in such a manner that the dynamics resulting from the interaction cannot be derived from simple multiplication of their individual dynamics.

While my system is intentionally general, the present results have broad implications for a variety of complex systems. I observed that: a) given spatial and temporal overlap, interacting factors demonstrating $1/f^{w}$, are not multiplicative but instead are best approximated by a gamma-distribution (Figure 16); b) the resultant spectral coefficient (either W_p or W_c) will tend to be less than the lowest of the interacting factors's w for one or two perturbations; c) increasing the number of simultaneous perturbations whose s are identical results in a modal shift to the right (Figure 14); d) factors with w values greater than 2.0, interacting with factors with w values less than 2.0, contribute to overall dynamics by altering the aggregate signal rather than shifting the mode of the distribution (Figure 15).

Herein I have demonstrated that "simple" power-law dynamics found in fractal systems can best be described by the more inclusive generalized gamma-distribution rather than the multiplicative power-law. The gamma-distribution has already been utilized to model fatigue and reliability life tests in which multiple components contribute to the mean time to failure (Crutcher et al. 1977). Similarly the gamma-distribution best describes many episodic events such as storm processes (Haggard et al. 1973), and the development of interior link-lengths in percolation networks (Shreve 1969; Stark 1991).

The gamma distribution is rarely reported for ecological and paleontological data analyses. This may be attributed to the need for large sample sizes (10,000 iterations in this study) and sufficiently fine-scale resolution relative to the mode to detect the gamma-distribution. For example, when data are lumped into coarse scales, which obscures any modal shift, the fit to a power-law distribution will improve. Thus the detection of a power-law behaviour does not necessarily imply a single causative factor nor do multiple

factors necessitate a gamma-distribution since a single factor may dominate the dynamics (Figure 14).

In an example drawn from paleontology, extinction dynamics at multiple biotic scales (e.g., species, genus and family) exhibit "1/*f*" dynamics (House 1989; Raup 1991; Kauffman 1993). Despite a myriad of perturbation factors that *can* lead to extinctions (e.g., sea-level fluctuations, climatic changes, volcanic activity), Raup (1991) argues that extinction dynamics at the geological timeframe are dominated by a single factor—meteorite (bollide) impacts. However, these mass extinction events account for only a small percentage (<5%) of all species extinctions (Plotnick and McKinney 1993). Maynard-Smith (1989) suggests that the majority of past (*background*) extinctions and diversity fluctuations have resulted from internal cascading biotic controls. Such background extinctions operate at high frequencies and thus are detectable only over finer time scales.

On an ecological timeframe, I have detected the signature of multiple interacting power-laws in model systems (in prep.). Colonization of new members into an assembling community is an exogenous perturbation which may induce cascading extinctions (collapses). The colonization of predators induces extinction magnitudes which follow a classic "1/*f*" distribution. Competitor colonizations however, yield extinction magnitudes which follow a gamma-distribution, suggesting multiple interacting power-laws due to cascading effects. Under such circumstances when the gamma-distribution is detected it is difficult, if not impossible, to deconvolve the gamma into the underlying component perturbations. At best one may approximate the number of component perturbations from the placement of the mode.

It has been suggested that power-laws are widespread in biology and may function as a general framework for describing a wide range of systems (Hastings and Sugihara

1993; Suki et al. 1994). These commonly detected power-laws tend to be *monofractal* , that is they have a single scaling exponent and are generally produced by a single source of perturbation (Lavallee et al. 1993). There are several recognized departures from complete fractality (Mandelbrot 1982; Hastings and Sugihara 1993). *Self-affine* systems exhibit statistical rather than exact self-similarity. *Multiscalar* systems can either exhibit self-similarity (or self-affinity) only over a portion of the range or have multiple self-affine regions which have different exponential parameters. These multiscalar systems will exhibit *phase transitions* (*sensu* Mandelbrot 1982) in which the disparity between regions in the distribution is sharply defined. In contrast, *multifractal* systems exhibit a change in the fractal dimension as the data is restricted above some threshold (Lovejoy and Schertzer 1991; Hastings and Sugihara 1993).

Conclusions

In contrast to the constraints of either monofractal or multiscalar models, most complex systems are governed by multiple factors operating simultaneously in either space or time. My results suggest that the typical analysis for fractal dynamics (reporting the slope over the linear portion of a log-log plot) may be inappropriate for multi-factor systems. Such an analysis ignores the information found in the modal shift relating to the number of interacting perturbations. This suggests that a new class of departure from complete fractality may be found in the interaction of multiple factors, best described by the gamma-distribution.

CHAPTER 6

Pattern in Ecological Systems

Introduction

A number of opposing ecological theories based upon the generalization of patterns found in natural, experimental, and model systems have been developed. Perhaps none is more hotly debated and divisive that the theories that support either equilibrial dynamics or non-equilibrial dynamics. This body of work explores the relative roles of of equilibrium and non-equilibrium dynamics in ecological systems. I find that non-equilibrium dynamics provide a better understanding of nature particularly since that the environment is constantly changing on some scale and thus ecological systems are always recovering from the last disturbance (Reice 1994; Whittaker 1995).

A variety of studies directly or indirectly implicate non-equilibrium dynamics as determinants of community organization. Surprisingly, some of these studies have been used to support equilibrium concepts (Simberloff 1974). For example, in Diamond's (1973) study of New Guinea birds, he concludes that the system in not in equilibrium due to disturbance from over 4,000 years prior. Simberloff and Wilson's (1969) classical study on colonization of defaunated islands showed that due to high invasion densities these systems were not in equilibrium. Studies of past climatic change events have shown that because species movement occurs at different rates, systems may be out of

equilibrium for extended periods (cf. Davis 1981). Furthermore, there are several consequences of equilibrial theory that cannot be reconciled with community responses to environmental variability (Wiens 1977).

In Chapter 2, I examined the influences of historical and environmental variability on competitive interactions. It was found that by modifying invasion history and environmental conditions, species numerical dominance could be altered. The phenomena of competitive exclusion (Diamond 1975), inhibition (Connell and Slatyer 1977), and "home field advantage" (Pimm 1989) are based on the establishment of a species which precludes a competitor from successfully colonizing that site. To examine this in experimental and model assembly systems, the role of history has become explicitly tested. It has been shown that priority effects and invasion sequence and timing are important factors in creating alternative states (Drake 1990a, 1990b).

In community assembly model studies, Drake (1990b, 1991) and others (Ginzburg et al. 1988; Hewitt et al. in press) found that, when species attempt to colonize extant communities one per time step at low density, complete invasion resistance would eventually occur. This does not agree with a number of studies of community dynamics of natural systems (Osman 1978; Carlton 1987, 1989; Bush and Whittaker 1993; Nichols et al. 1993; Hewitt 1993; Reice 1994; Robinson et al. 1995). There are a number of problems using single species invading at low densities including Allee effects, facilitation, and trophic accommodation. Thus, felt that complete invasion resistance was an offshoot of the equilibrium mindset. To examine whether complete invasion

resistance was a result of model assumptions, I examine the influence of invasion sequence, timing, and density in experimental and model systems.

In Chapter 2, I examine the role of various invasion factors on community assembly including invasion density. It was found that increasing invasion density could lead to alternative states of community structure. To expand upon this, I examined whether the equilibrial pattern of complete invasion resistance found in assembly models would hold under increasing both the inoculation densities and number of species invading per time in Chapter 3. When these two factors were varied, complete invasion resistance did not occur, instead there were periods of stasis intermixed with species' colonizations and extinctions.

The lack of complete invasion resistance and the increased colonization success with higher rates and densities of invading species lead me to question the validity of island biogeographic theory for assembling systems. In fact, MacArthur and Wilson (1967) suggested that their theory may not hold for successional (assembling) systems. Thus, in Chapter 4, I used the same assembly model as in Chapter 3, but increased the rates of species invasions allowing up to 10 species to invade per time step.

Increasing the rate of species invasions allowed for the testing of island versus mainland dynamics. Distant islands have lower rates of immigration than do near islands or mainland communities and thus are more likely to exhibit greater invasion resistance. Yet, community assembly and invasion theory of mainlands are mostly based upon studies of distant islands. Island biogeography theory (MacArthur and Wilson 1967)

predicts that there is a dynamic equilibrial number of species in systems and that this is regulated by colonization and extinction rates. However, I found that with increasing invasion rates, no dynamic equilibrium occurred agreeing with studies of natural systems (Abbott and Grant 1976; Osman 1978; Keough and Butler 1983; Osman and Whitlach 1978; and Osman and Dean 1987). The use of island biogeography theory for assembling systems does not fit as MacArthur and Wilson (1967) stated it would not for successional systems. Thus, new models and theories for mainland systems need to be developed and tested, I believe that Chapter 4 is a start for that process.

A critical aspect of understanding ecological pattern necessitates the choice of appropriate observational temporal and spatial scales. Chapter 5 is a cautionary chapter dealing with large scale spatial patterns. Since Mandelbrot's book (1982) on fractals in natural systems, a number of recent papers have attempted to demonstrate fractal and power law distributions. In fact, I have co-authored several of these papers (Drake et al. 1992; Kolasa et al. in prep). Power law distributions have been found for extinction dynamics at coarse, large scales (Raup 1986, 1991; House 1988; Plotnick and McKinney 1993). Such distributions are suggestive of underlying self-similar spatial structure. However, for ecological time frames and spatial scales I believe that these distributions can be more complex. For instance, if multiple perturbations are acting upon a system, the pattern may tend towards a normal distribution. This occurs due to overlapping distributions of larger disturbances and the cumulative effects of small ones in finite systems.

To test this, I developed a model to allow multiple perturbations of differing power law coefficients to interact on a landscape. It was found that depending upon the number of and spectral coefficient of the perturbations the resultant magnitude frequency distribution could range from a power law to a gamma distribution as predicted. Thus, the finding of or lack of a power law distribution may not always provide information concerning the system without a good deal of knowledge of it.

I believe that ecological theory must go in the direction of incorporating non-equilibrial dynamics. Two key factors in this push are global climatic change and increased species movements. Studies of past climatic change events have demonstrated that unique communities may form (Van Devender 1980) and species movement rates vary greatly (Davis 1981). Global climate models predict widespread changes in temperature and precipitation patterns resulting from the effect of increasing CO_2, methane, and other greenhouse gases. The predicted rate of climate change is at least an order of magnitude greater than past rates. As a result, communities will and perhaps are undergoing drastic changes.

Along with the changes occurring due to climate change are those due to anthropogenic activities and transport mechanisms. Thus these movement patterns continue to reduce the isolation of regional biotas from one another, the numbers of species and inoculation densities of invaders will increase. This will undoubtedly result in higher susceptibilities to invasion in recipient regions and communities along with

concomitant non-equilibrium dynamics (i.e. higher order interactions of Billick and Case 1994 and Wooten 1994).

Both climate change and human mediated transport of species must overcome biological inertia. Non-equilibrial dynamics will better allow for short term predictability which is required for conservation of species that are (or will be) currently rare, threatened, and endangered. To conserve species one must know or be reasonably informed in what steps and what degree of management are necessary.

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Appendix

Table 1. Summary of Experiments

Experiment	Variables Altered and Tested
1	Growth rates and resource efficiency
2	Invasion sequence and timing
3	Invasion inoculation density
4	Allelopathy and nutrient depletion
5	Water column mixing
6	Continuous nutrient inputs and invasion sequence

Table 2. Growth rates, resource depletion rates, and resource efficiencies

Species	10 Day			18 Day			25 Day		
	dN/dt	dR/dt	RUE	dN/dt	dR/dt	RUE	dN/dt	dR/dt	RUE
Chlamydomonas	0.626^{a}	0.278^{a}	2.25^{c}	0.369^{b}	0.258^{a}	1.43^{d}	0.166^{d}	$0.262^{a,b}$	0.63^{c}
Ankistrodesmus	0.095^{c}	0.086^{c}	1.10^{d}	0.326^{c}	0.115^{b}	2.83^{b}	0.201^{c}	0.253^{b}	0.80^{b}
Selenastrum	0.605^{a}	0.102^{b}	5.93^{a}	0.365^{b}	0.090^{c}	4.06^{a}	0.258^{a}	0.270^{a}	0.97^{a}
Scenedesmus	0.295^{b}	0.090^{c}	3.28^{b}	0.401^{a}	0.239^{a}	1.68^{c}	0.223^{b}	0.270^{a}	0.83^{b}

Table 3. Summary results of numerical dominance or codominance based on average densities for various experimental conditions for four competing species of green algae. Numerical dominance or codominance is indicated by X. *Chlamydomonas*, *Scenedesmus*, *Selenastrum*, and *Ankistrodesmus* are abbreviated by CHL, SCE, SEL, and ANK, respectively.

	Numerically Dominant Species			
EXPERIMENT	SCE	SEL	CHL	ANK
Experiment 2				
Static simultaneous invasion	X			
10 day interval				
All sequences	X			
15 day interval				
ANK invaded first				X
SCE invaded first	X			
SEL invaded first		X		
CHL invaded first	X			
Experiment 3				
10 day interval				
All sequences	X			
15 day interval				
ANK invaded first				X
SCE invaded first	X			
SEL invaded first		X		
CHL invaded first			X	
Experiment 4				
10 day interval - no nutrient addition				
ANK filtrate			X	
SCE filtrate			X	
SEL filtrate			X	
CHL filtrate			X	
15 day interval - N and P addition				
ANK filtrate			X	
SCE filtrate	X			
SEL filtrate			X	
CHL filtrate			X	
Experiment 5				
All sequences		X		
Experiment 6				
Control	X			
Treatment 1	X			
Treatment 2	X	X	X	

Table 4. Average growth rates for each species in filtrate from each species based upon 15 days of growth after inoculation into the filtered medium which had nitrogen and phosphorus levels adjusted to full medium strength. Different letters indicate significant differences between column values, while same letter indicates no signifcant difference.

Invader Species Filter Species	*Selenastrum*	*Scenedesmus*	*Chlamydomonas*	*Ankistrodesmus*
Selenastrum	0.247[a]	0.251[a]	0.282[a]	0.255[a]
Scenedesmus	0.215[b]	0.214[b]	0.216[b]	0.220[b]
Chlamydomonas	0.154[c]	0.190[c]	0.167[c]	0.176[d]
Ankistrodesmus	0.213[b]	0.181[d]	0.214[b]	0.194[c]

Table 5. Average and standard deviation are given for each level of immigrant under the fixed number of immigrants scenario. Letter denotes statistcial similarity or difference between levels as tested for by T-method.

	Level of Immigration							
	2	3	4	5	8	10	df	F
Colonization Rate	a	b	c	d	e	f	5	272.3***
Average	0.46	0.57	0.78	0.96	1.36	1.65		
SD	0.046	0.123	0.085	0.093	0.095	0.073		
Colonization Probability	a	b	b	b	b	b	5	9.6***
Average	0.229	0.189	0.196	0.192	0.171	0.165		
SD	0.023	0.041	0.021	0.019	0.023	0.007		
Extinction Rate	a	b	c	d	e	f	5	272.5***
Average	0.45	0.56	0.77	0.95	1.36	1.64		
SD	0.049	0.123	0.084	0.095	0.093	0.072		
Turnover Rate	a	b	c	d	e	f		
Average	0.46	0.56	0.78	0.96	1.36	1.64	5	272.9***
SD	0.047	0.123	0.084	0.093	0.093	0.072		
Average Diversity	a	b	b	b	b	b	5	19.3***
Average	3.49	4.97	4.94	4.99	4.62	4.58		
SD	0.435	0.713	0.378	0.315	0.255	0.121		

Table 6. Stochastic boundedness data for the fixed number of immigrants scenario.

	Level of Immigration					
	2	3	4	5	8	10
CVpop						
Avg	73.358	71.984	70.339	74.204	80.932	85.598
SD	5.131	5.090	4.920	2.980	4.152	2.609
SEcv						
Avg	3.585	3.472	3.340	3.644	4.248	4.695
SD	0.425	0.430	0.399	0.250	0.396	0.266
t						
Avg	16.247	16.379	16.528	16.180	15.488	14.986
SD	0.491	0.494	0.459	0.290	0.446	0.287
ω						
Avg	0.617	0.604	0.592	0.621	0.671	0.700
SD	0.037	0.037	0.036	0.021	0.029	0.017

Table 7. Average and standard deviation for each level of immigrant under the variable number of immigrants scenario.

	Level of Immigration											
	1	2	3	4	5	6	7	8	9	10	df	F
Colonization Probability												
Per Invader	a	a	a,b	a,b	a,b	a,b	a,b	b	b	b	9	3.38**
Average	0.249	0.249	0.213	0.199	0.201	0.200	0.193	0.171	0.188	0.189		
SD	0.064	0.049	0.031	0.047	0.031	0.038	0.038	0.024	0.043	0.045		
Colonization Probability												
Per Time Step	a	b	b,d	b,c	c,e	c,e	c,d,e	c,e	c,e	e	9	16.02***
Average	0.249	0.354	0.393	0.425	0.483	0.488	0.512	0.471	0.500	0.525		
SD	0.064	0.069	0.044	0.080	0.050	0.070	0.073	0.050	0.071	0.101		
Extinction Probability	a	a	a,b	b,c	b,c,d	c,d,e	c,d,e	e	d,e	b,c,e	9	17.71***
Average	0.059	0.093	0.123	0.165	0.183	0.221	0.229	0.270	0.246	0.195		
SD	0.042	0.031	0.041	0.048	0.046	0.059	0.060	0.075	0.072	0.061		
Average Extinction Size	a	b	b	a,b	b	b	b	b	b,c	c	9	7.31***
Average	8.21	6.09	5.74	6.50	6.00	6.22	5.38	5.45	4.56	3.21		
SD	2.055	2.525	1.045	1.323	1.545	1.414	1.048	0.959	1.237	1.261		
Turnover Probability	a	b	b,c	c,d	d,e	e	e	e	e	e		
Average	0.314	0.448	0.524	0.597	0.663	0.717	0.751	0.749	0.744	0.726	9	43.76***
SD	0.075	0.073	0.036	0.079	0.067	0.075	0.049	0.050	0.074	0.090		

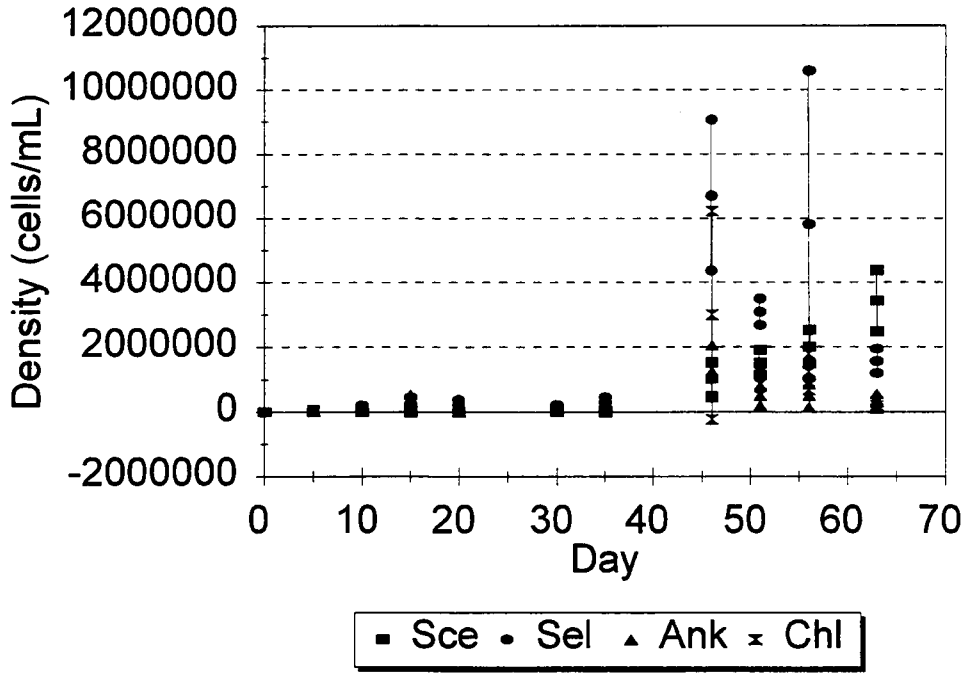


Figure 1. Average densities of each species over time in continuous flow microcosms for the control treatment. In the control, all species were introduced simultaneously. Abbreviations of species are same as in Table 2. The average and average plus and minus the standard deviation are given for each.

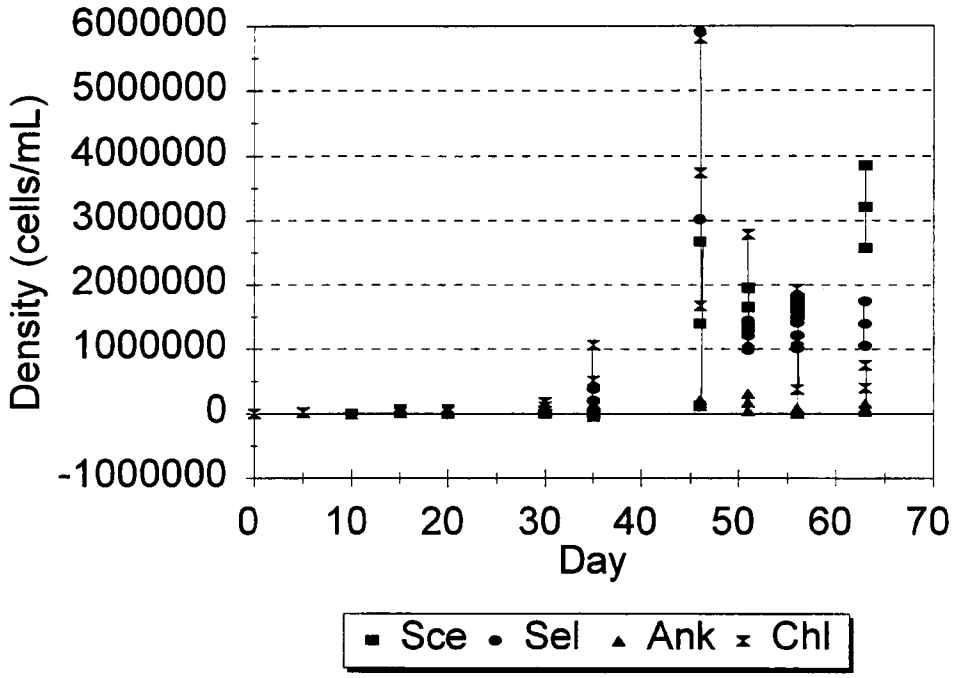


Figure 2. Average densities of each species over time in continuous flow microcosms for treatment 1. In this treatment, the order of invasion was *Chlamydomonas*, *Selenastrum*, *Ankistrodesmus*, and *Scenedesmus*. The interval between invasion was ten days. Abbreviations of species are same as in Table 2. The average and average plus and minus the standard deviation are given for each.

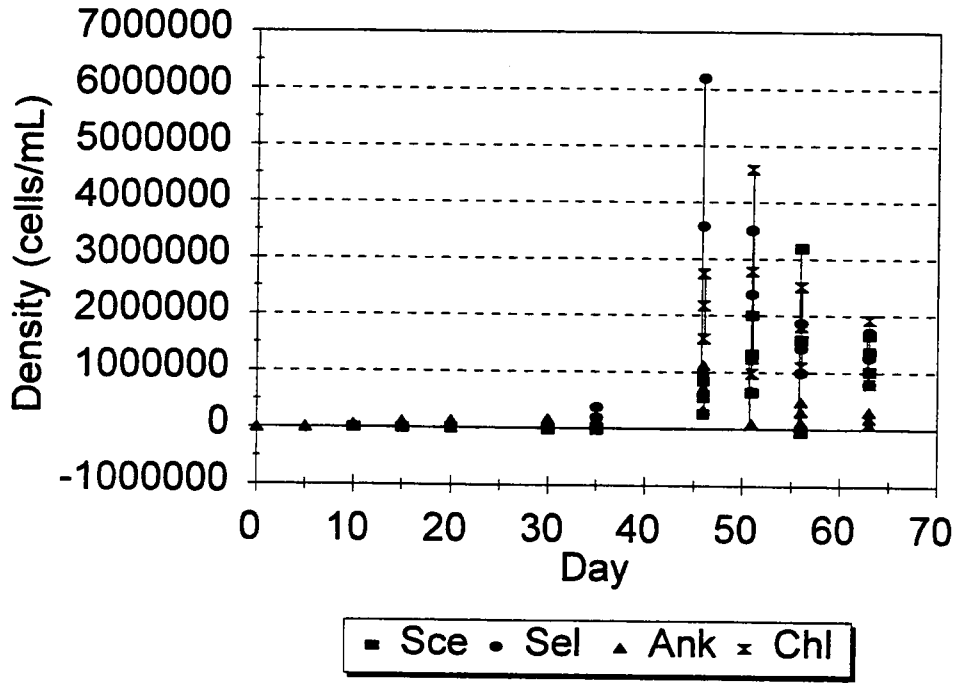


Figure 3. Average densities of each species over time in continuous flow microcosms for treatment 2. In this treatment, the order of invasion was *Ankistrodesmus*, *Scenedesmus*, *Selenastrum*, and *Chlamydomonas*. The interval between invasion was ten days. Abbreviations of species are same as in Table 2. The average and average plus and minus the standard deviation are given for each.

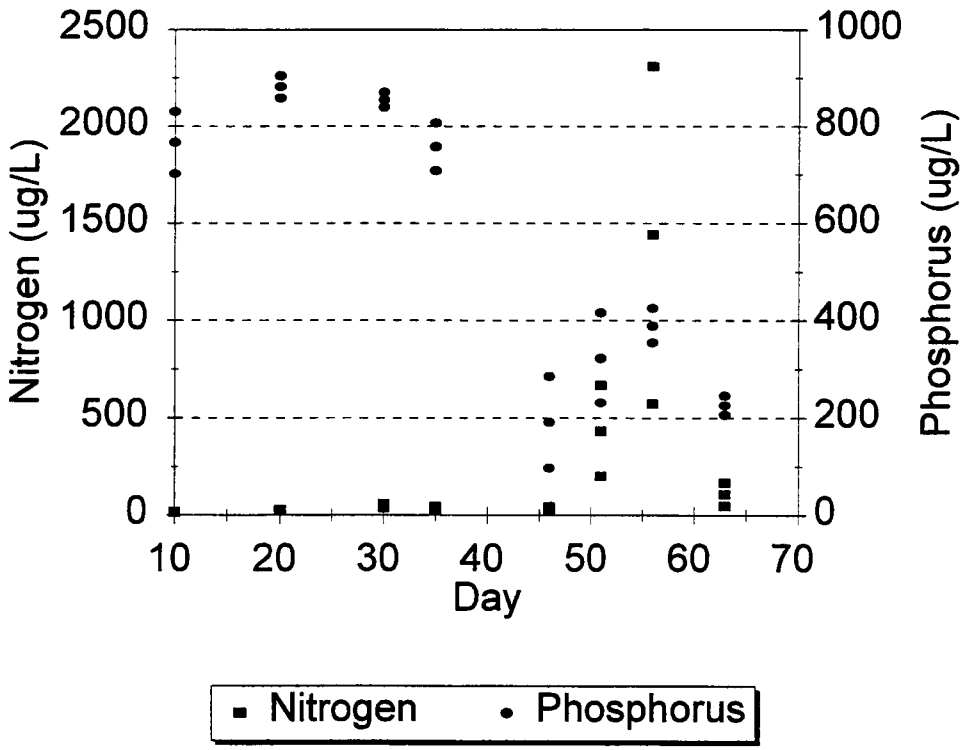


Figure 4. Nitrogen (nitrate-nitrate) and phosphorus dynamics in control. Abbreviations of species are same as in Table 2. The average and average plus and minus the standard deviation are given for each.

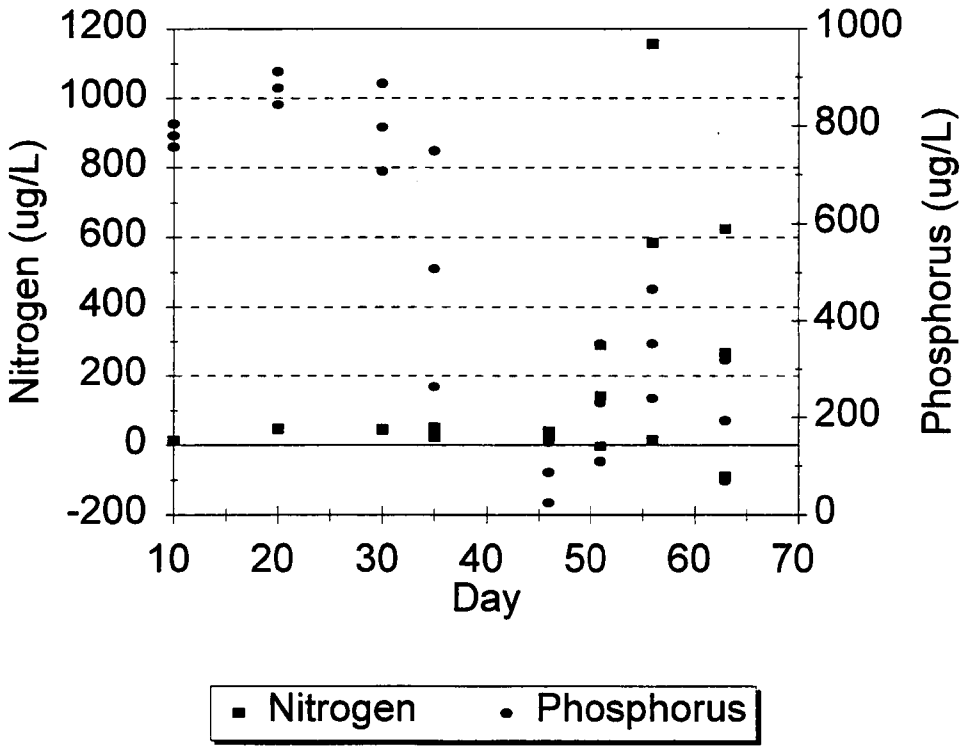


Figure 5. Nitrogen (nitrate-nitrate) and phosphorus dynamics in treatment 1. Abbreviations of species are same as in Table 2. The average and average plus and minus the standard deviation are given for each.

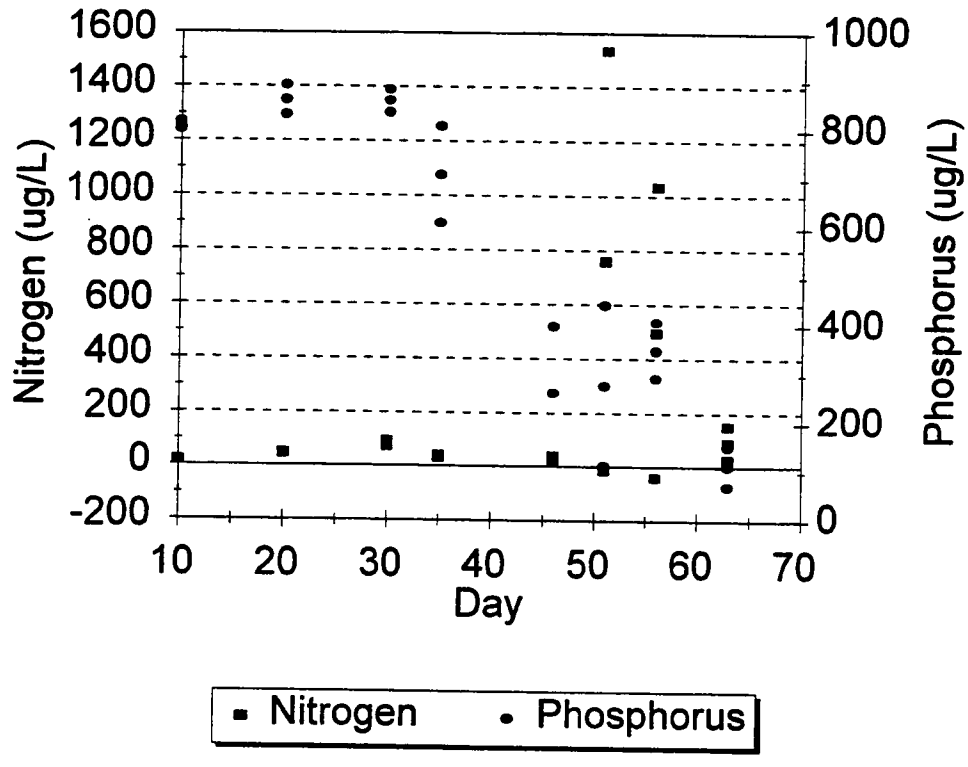


Figure 6. Nitrogen (nitrate-nitrate) and phosphorus dynamics in treatment 2. Abbreviations of species are same as in Table 2. The average and average plus and minus the standard deviation are given for each.

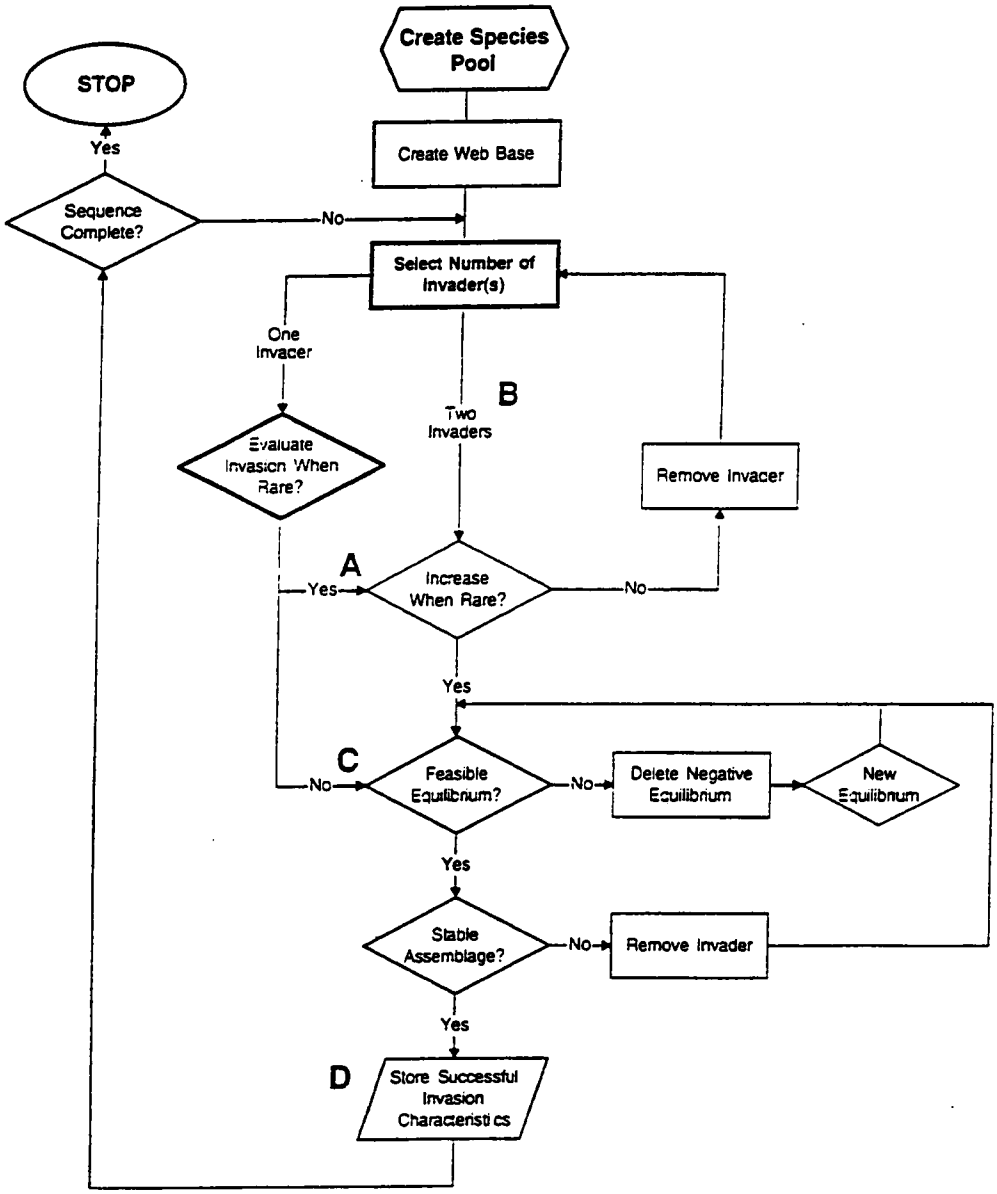


Figure 7. A flow chart of the general assembly model. **A** denotes the pathway for scenario A where single species invade at low inoculation densities. **B** denotes scenario B where two species attempt to invade the extant community at low inoculation densities. **C** denotes scenario C where single species invade at inoculation densities near their equilibrium. **D** denotes the point at which colonization success is evaluated.

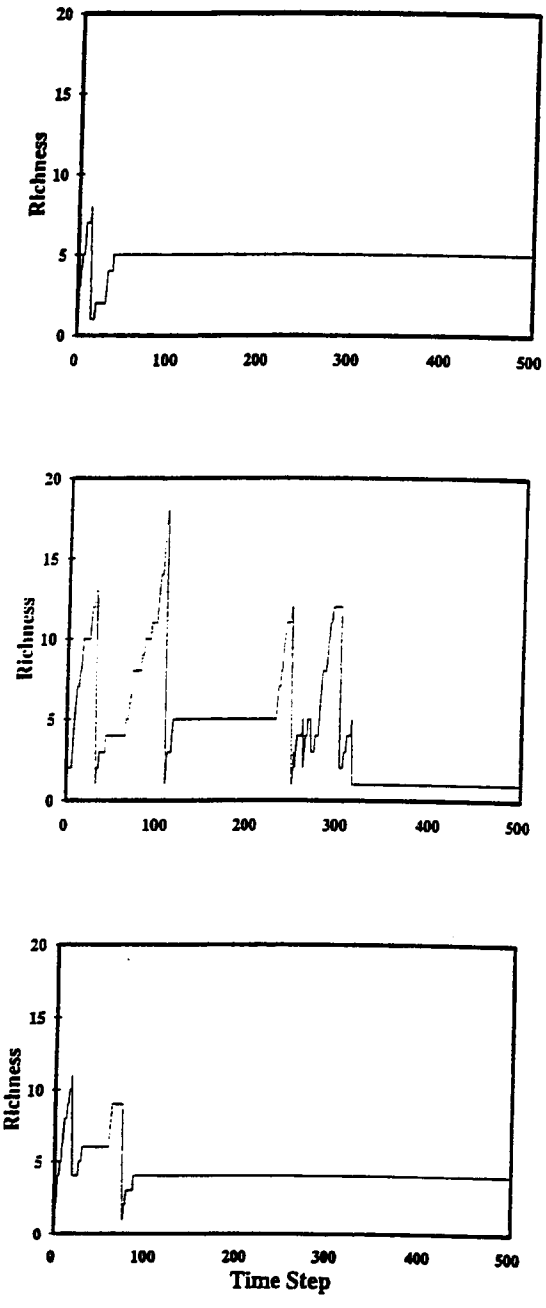


Figure 8. Changes in richness over time during community assembly under scenario A for three typical simulations. The communities differed in species composition and richness due to differences in invasion history. All communities assembled under the assumptions of single species invading at low densities resulted in complete resistance.

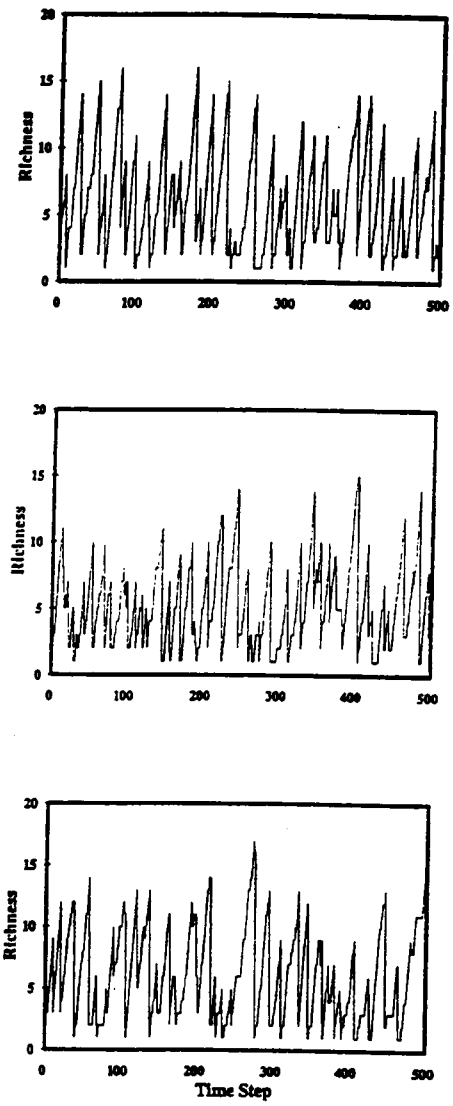


Figure 9. Changes in richness over time during community assembly under scenario B for three typical simulations. No communities assembled with two species invading per time resulted in complete invasion resistance, but note that there are periods of stasis in each of these simulations.

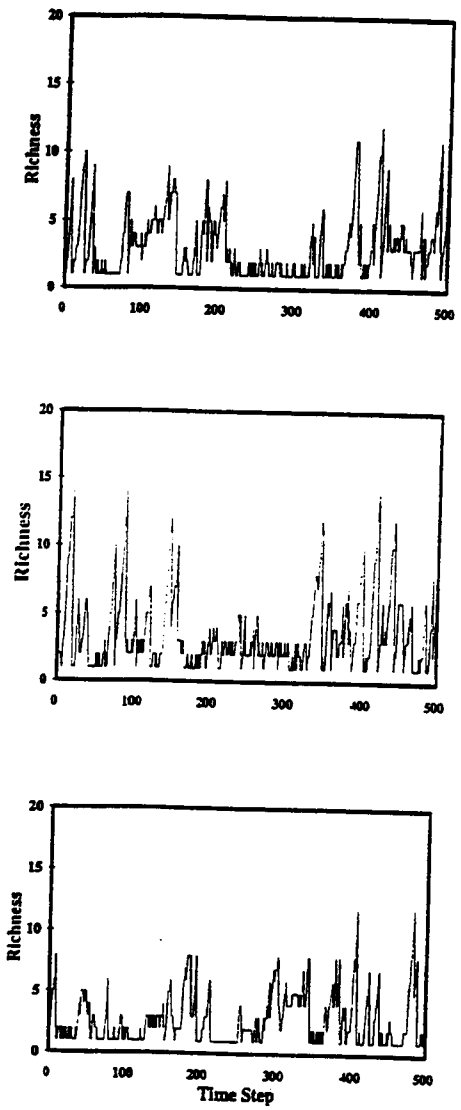


Figure 10. Changes in richness over time during community assembly under scenario C for three typical simulations. No communities assembled with single species invading at high inoculation densities led to complete invasion resistance, but note that there are periods of stasis in each of these simulations.

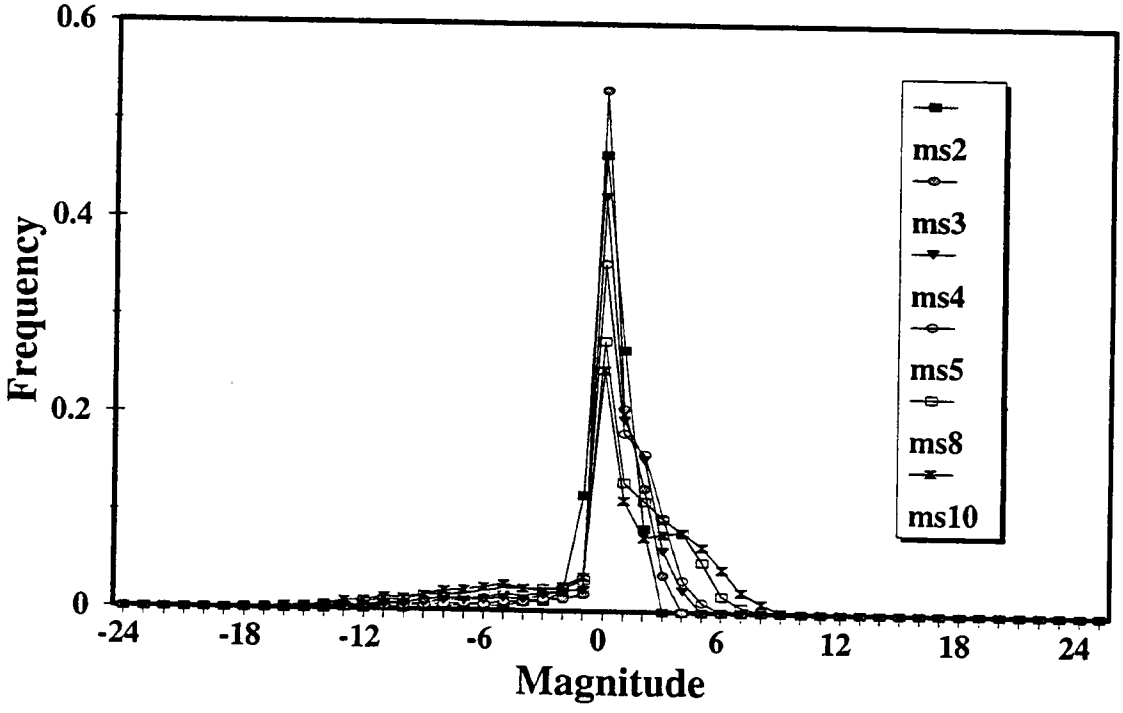


Figure 11. Probability of magnitude of net turnover, colonization minus extinction, shown for each level of immigrating species. Note that the most prevalent size event was zero and increasing turnover with immigration level.

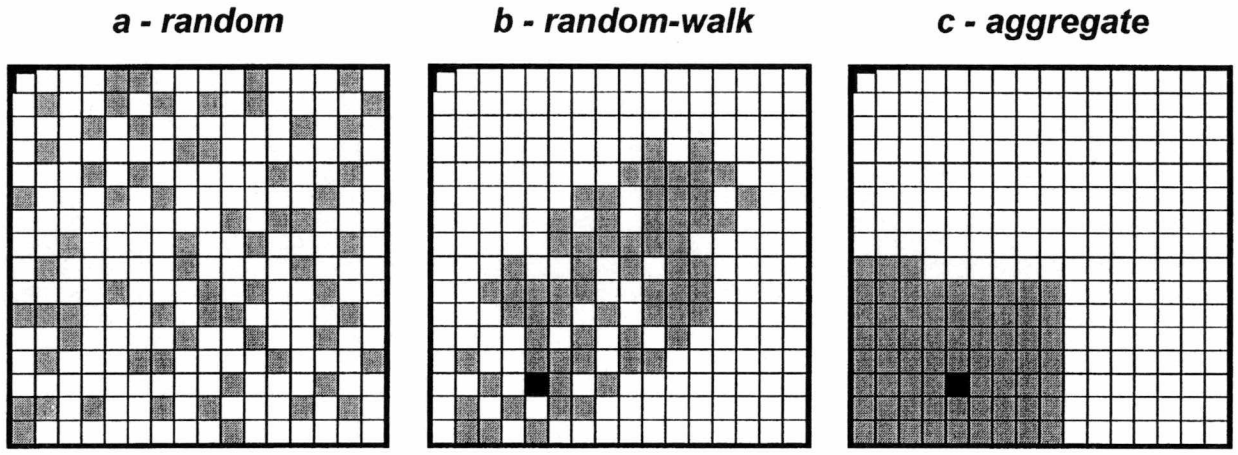


Figure 12. *a, b, c,* Placement of disturbed patches from a single perturbation on a 16X16 lattice (landscape) following three disturbance dispersion patterns. Initially the landscape is saturated (complete occupancy) and the perturbation induces patch extinctions (collapse denoted by light grey patches). Unperturbed patches are not shaded. Here the disturbance magnitude is 66 patches for each dispersion type. Patches were selected from the 256 possible patches without replacement either randomly (*a*), or by randomly selecting a seed site (here identified by the dark grey patch in *b* and *c*) and performing either a random-walk (*b*) or aggregate (*c*) movements from the seed site.

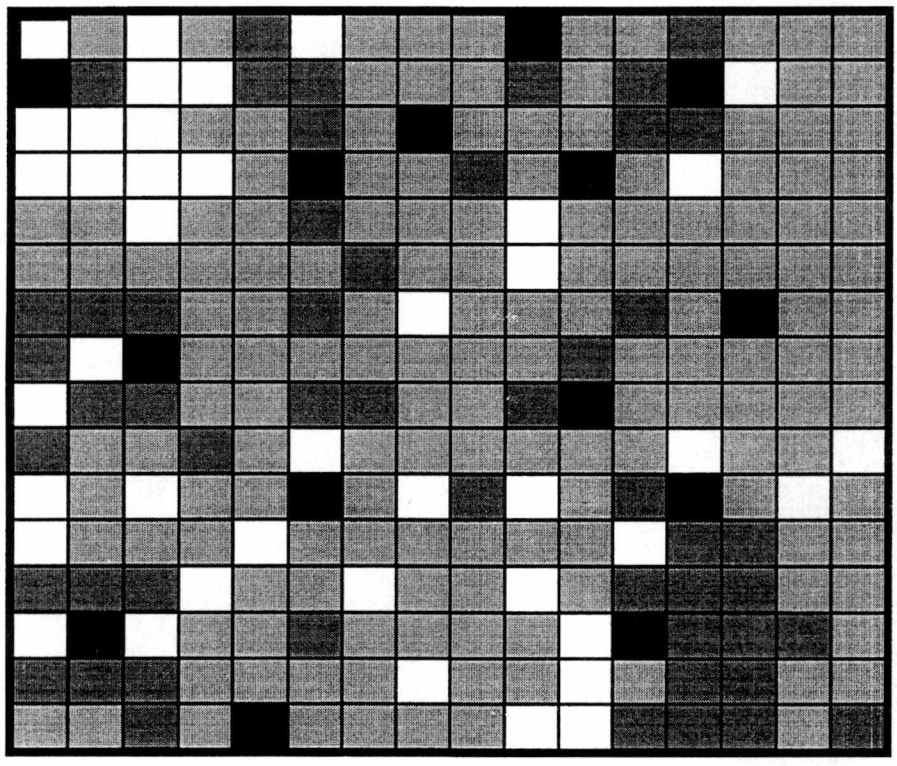


Figure 13. Output diagram of a single iteration for two interacting perturbations. Collapses from each perturbation signal were randomly placed on a 16x16 landscape, such that collapses from different perturbations could overlap. Collapse magnitudes from the two interacting perturbations are drawn from a $1/f^{1.0}$ distribution (signal 1: light grey; signal 2: dark grey). Patches perturbed simultaneously by both perturbations are denoted as interaction patches (black). Unperturbed patches (undisturbed) are not shaded. In this example, the total collapse magnitude is 198 patches (signal 1: 164 patches; signal 2: 65 patches; 14 interacting patches).

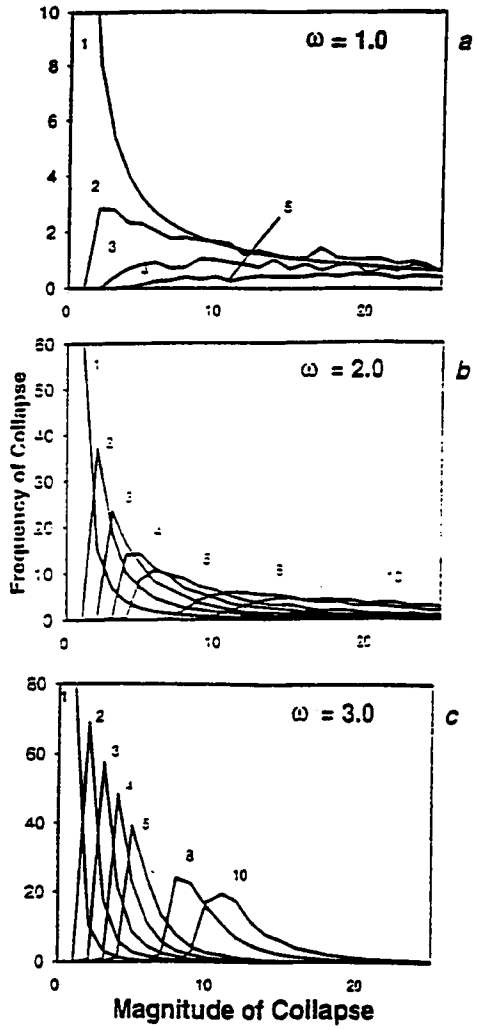


Figure 14. *a, b, c,* Effects of interactions between multiple $1/f$ perturbations having the same value and randomly placed collapses. The numbers next to the lines represent the number of interacting perturbations. All perturbations are identical within a graph with ω= to 1.0 (*a*), 2.0 (*b*), and 3.0 (*c*). These values were employed because it has been suggested that in most systems ranges between 0 and positive 2.0. Note the changes in Y-axis scales between *a, b,* and *c*. For ω=1.0 a decrease in the aggregate spectral coefficient occurs as the number of interactions increase and above four interactions it becomes negative (a positive slope). For ω=2.0 and 3.0, the change in aggregate spectral coefficient as the number of interactions increase is not as fast nor as extreme (Table 1) instead the mode shift is more evident.

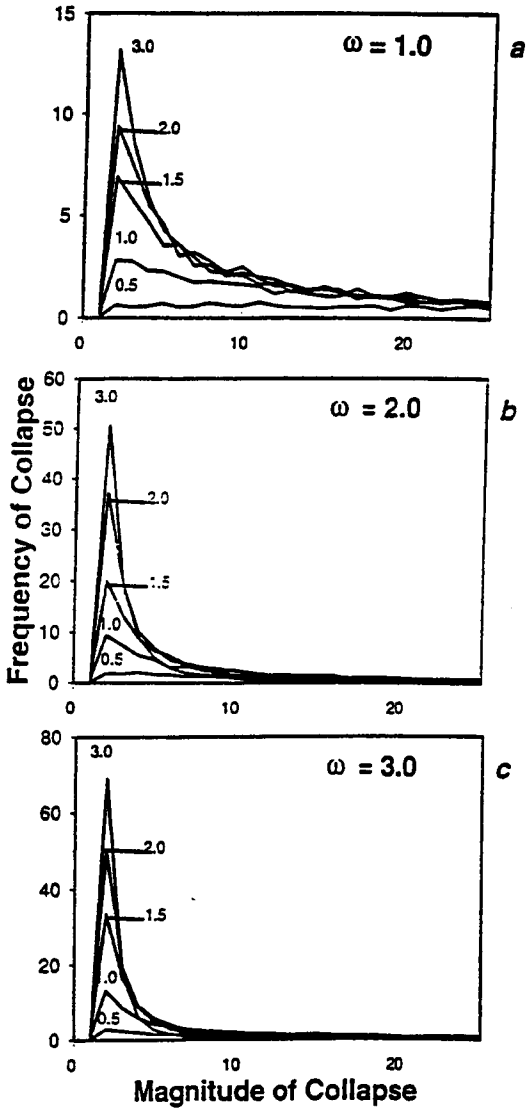


Figure 15. *a, b, c,* Effects of interactions between two *1/f* perturbations. In panels *a, b,* and *c,* 1/f perturbations of 1.0, 2.0 and 3.0 (respectively) interact with a second signal whose ω value is given next to the respective lines. Note the changes in Y-axis scales between *a, b,* and *c*. As the difference between the two s increases the signal with the smaller ω dominates the aggregate spectral coefficient (Table 1). Thus for a $1/f^{0.5}$ perturbation interacting with perturbations in which ω=1.0 (*a*), 2.0 (*b*), or 3.0 (*c*) the resultant curve is not altered in shape. In contrast for a $1/f^{3.0}$ perturbation the curve is altered by each interacting signal.

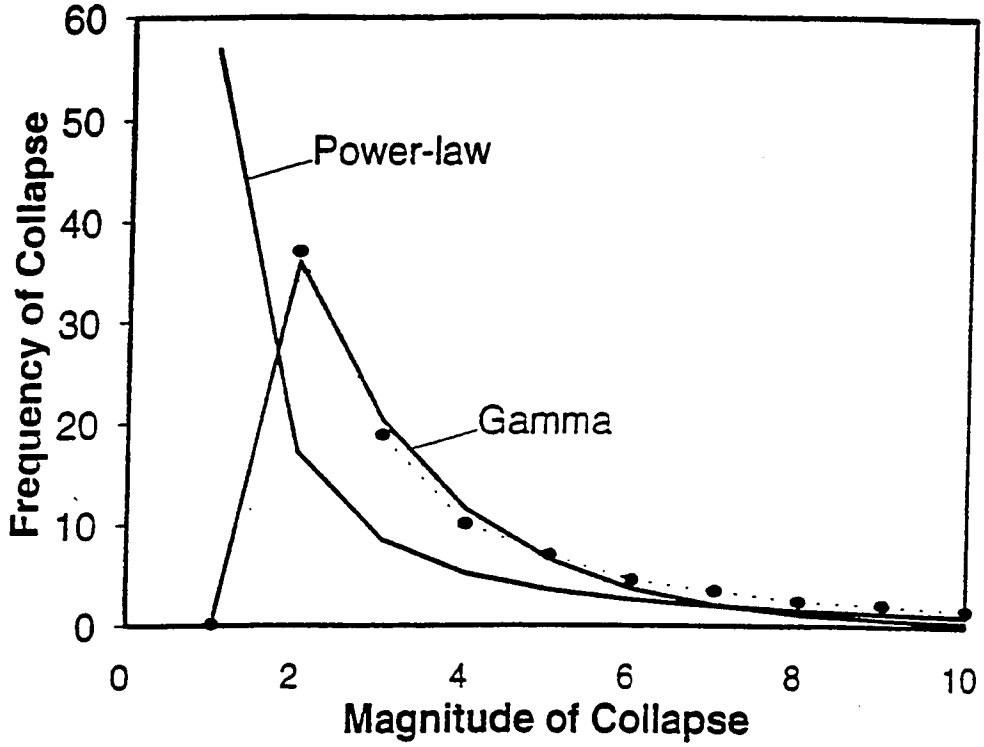


Figure 16. Frequency analysis of data from a Monte Carlo simulation with 2 interacting $1/f^{2.0}$ perturbations. Both the power-law distribution and four parameter gamma-distribution were fit to the data curve by non-linear least squares regression. The power-law fit resulted in a slope (spectral coefficient Ω_c) of 1.789 (r^2=0.729) while the gamma-distribution fit resulted in a much closer approximation to the data curve (r^2=0.990).

VITA

I was born in Hamilton, Ohio on October 2, 1961. I attended public and private schools in Ohio until the tenth grade, moving to Phoenix, Arizona to finish high school at Shadow Mountain H.S. in 1980. I briefly attended Phoenix College, a small junior college before moving back to Ohio and working. I then spent three years in the Army and another year as a civilian working for the Army. Eventually, I ended back in Arizona graduating from Arizona State University with a B.S. in Biology (with Honors) in 1989. I worked for a small environmental company in Scottsdale, Arizona before moving to Knoxville to enter graduate school in the Graduate Program in Ecology at the University of Tennessee in 1990. I received my doctoral degree (Ph. D. in Ecology) in December of 1995.