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The influence of loss of diversity on community dynamics and ecosystem functioning has recently received considerable attention. Although study of biodiversity has a long history within ecology, empirical investigations exploring consequences of loss have been rare. Because many factors confound diversity comparisons, experimental manipulations of diversity offer the most direct way of attributing cause to diversity loss.

The effects of reduction in number of species will depend on the strength and sign of species interactions affected by loss of diversity. An experiment performed on a high zone, rocky intertidal community in which macroalgal diversity was manipulated demonstrated that effects of diversity loss will be highly dependent on which species are removed. However, effects of diversity reductions were strongest at the harsh end of a stress gradient where interactions were more positive. Thus, factors that affect the

strength and sign of species interactions such as the degree of physical stress may serve as a rough guide to where the effects of diversity loss will be most severe.

An assessment of the influence of diversity on community response to a strong physical perturbation was performed using an experimentally-induced thermal stress. Higher diversity treatments were most strongly affected directly by the stress because such treatments had higher abundance and therefore more biomass to lose. However, those same treatments recovered more quickly from the stress. Community recovery of initially low diversity treatments was slowed by persistence of non-typical states or slow recovery of dominant species.

A simulation study was performed to assess the ability of different experimental designs to detect biodiversity effects. Our ability to predict consequences of changes in diversity will be dependent on our ability to distinguish the most influential biodiversity "components" within a system. This study uncovered a phenomenon that will be common in biodiversity studies: misidentification of one biodiversity component (e. g., an effect of a keystone species) as a different component (e. g., an effect of the number of species). I call this phenomenon "aliasing." Because of the complexity of biodiversity, experiments and observational studies will be highly susceptible to aliasing and, thus, results will require careful interpretation.

The Ecological Consequences of the Reduction of Species Diversity: Experimental Approaches

by

Gary William Allison

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Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Gary William Allison, Author

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This dissertation is dedicated
to my mother
and the loving memory of my father

The Ecological Consequences of the Reduction of Species Diversity: Experimental Approaches

CHAPTER 1

General Introduction

BACKGROUND

The diversity of organisms has long fascinated biologists and has prompted them to compare and classify organisms (Linnaei 1758, Cuvier 1833) and to postulate mechanisms for the source of the variation (Lamarck 1809, Darwin 1859). During the latter part of this century, ecologists have adopted diversity as a central theme, addressing such topics as geographical patterns of diversity (Vermeij 1978, Rex 1981, Ricklefs and Schluter 1993), factors that influence diversity (Hutchinson 1959, Connell and Orias 1964, Paine 1966, MacArthur and Wilson 1967, Rosenzweig 1971, Menge and Sutherland 1976, Connell 1978, Lubchenco 1978, Hixon and Menge 1991, Tilman and Pacala 1993, Huston 1994) and how diversity of a system influences other characteristics of communities and ecosystems (MacArthur 1955, Elton 1958, May 1973, Pimm 1984, Schulze and Mooney 1993a, United Nations Environment Programme 1995, Mooney et al. 1996).

The topic of the functional significance of diversity has spawned much speculation and one hypothesis has been historically influential: that species diversity increases a system's stability. The paradigm that "diversity begets stability" was long accepted within ecological thought (Clements 1936, Allee et al. 1949, Odum 1953, Hutchinson 1959). In the 1950's, MacArthur's (1955) conceptual framework and Elton's (1958) five lines of evidence seemed to strengthened faith in the tenet (Hutchinson 1959). A challenge to this idea was established by May (1971, 1972, 1973; see also MacArthur 1970) when he showed that stability was not a direct consequence of the model systems he assembled; indeed, more complex food-web models were less stable than simple ones. This was not particularly a challenge to the idea that naturally diverse systems were more stable, as May (1971) notes, only that their stability was *caused* by their complexity. However, May's work sparked a large body of theoretical work that explored the relationship of complexity and stability in model systems (e. g., Harrison 1979, Pimm 1979, 1980, 1982, Nunney 1980, Armstrong 1982). These studies often concluded that species diversity inversely affected the community dynamics usually associated with "stability." Much of this early work was within the context of food web theory (Winemiller and Polis 1996) and Lotka/Volterra models. Throughout early discussions, there was much debate about what aspects of the dynamics of communities and ecosystems that "stability" really meant (Lewontin 1969, Margalef 1969, Holling 1973, Orians 1975, McNaughton 1977).

However, in this earlier work, empirical evidence of the causal relation of diversity to stability in natural systems was slight. Some of the few examples included Watt's (1964) work that used forest/insect surveys to suggest that a predator population is

less numerically stable when the trophic level below it is more diverse, challenging the MacArthur (1955) hypothesis. On the other hand, McNaughton (1977) cited his own work in the Serengeti on grazer effects and the work of others (Hurd et al. 1971, Mellinger and McNaughton 1975) on fertilizer perturbations in old fields as evidence to support the hypothesis. All of these studies involved comparisons between sites that differed naturally in diversity. Therefore, because diversity was not explicitly manipulated, confounding causes for the results could not be ruled out. To that point, Murdoch (1975) suggested that the causes of differences in diversity, such as habitat heterogeneity, were also responsible for the differences in stability and that species diversity was merely correlated with the actual cause.

In the early phases of this research, a few direct manipulations of diversity in different systems had found some evidence of causal links between diversity and stability. The experiments of Hairston et al. (1968) using protozoan/bacterial microcosms showed that diversity of prey increased the stability of predators in some but not all predator combinations. Pimentel (1961) found that mixed species plantings prevented insect pest outbreaks. Root (1973) manipulated the diversity of the vegetation surrounding collard crops and found that herbivore load was highest in a monoculture and thus more likely to cause pest outbreaks.

In general, however, theoretical work on the topic far outweighed empirical studies, perhaps because much of the theory was difficult to operationalize to real systems (DeAngelis and Waterhouse 1987, Peters 1991). By the mid 1980s, the perceived contradictions, the lack of empirical research and large confusion of defining terms arguably caused the field to stagnate (McNaughton 1977, Peters 1991).

CURRENT CONTEXT

Within the last decade, concerns about the impacts of humans on biotic diversity has revived and transformed questions of the importance of diversity and has fostered attempts to characterize diversity and to predict how humans affect diversity. This attention has been focused by a growing concern for the tremendous impact that humans have had on biotic diversity, both intentionally and unintentionally (Lubchenco et al. 1991, United Nations Environment Programme 1995, Vitousek et al. 1995, Mooney et al. 1996, Orians et al. 1996). Thus, this more recent work has assumed the challenge not only of understanding the importance of diversity, but also for developing knowledge to predict the consequences of changes in diversity.

While earlier work was often focused on species diversity (i. e., richness and evenness), usually within a food web context (Winemiller and Polis 1996), newer work is considering numerous "components" of biotic diversity. These range from the number of species within a functional group to the number of functional groups, from structural diversity to phyletic diversity, and from genetic diversity to ecosystem diversity. This fundamental expansion of the scope of "diversity" has broadened the focus from "Does high diversity stabilize systems?" to "What aspects of diversity are important and under what conditions?" (McNaughton 1993). The responses that are used to explore the importance of diversity have also expanded from community dynamics to include "ecosystem functioning" such as biogeochemical cycling and primary productivity. Furthermore, there has been an expansion to include not only how high diversity systems differ from low diversity systems, but also how the *loss* (or gain) of diversity will affect a

given system. This expansion of scope reflects, in part, the assertion by biologists that biotic diversity will be important in many different ways as well as the somber responsibility to determine how these different aspects of diversity are being modified by humans and, further, to predict the consequences of current and future modifications of diversity. It must be noted from the outset, however, that there are numerous reasons to conserve species, from ethical reasons to reasons of their potential for genetic engineering or pharmaceutical research. While an understanding of the ecological consequences of species loss may illustrate more tangible implications of human actions, such consequences should not be the sole criteria for conservation decisions.

There are several ways in which these questions may be approached. There are theoretical and conceptual models of the effects of the loss of diversity (e. g., Tilman et al. 1994). While this work is an important extension of earlier work, perhaps the most exciting change in recent diversity studies has been the strong emphasis on empirical research. Observational studies on large scales have been used to suggest the effects of diversity (e. g., Frank and McNaughton 1991, Schulze and Mooney 1993a, Davis and Richardson 1995, Vitousek et al. 1995, Mooney et al. 1996, Orians et al. 1996, Silver et al. 1996). The comparative/experimental approach in which similar experiments are performed in areas of different diversities have been useful in a number of situations (see McNaughton (1993) for a review). Some recent tests of effects of diversity loss have been performed by indirectly manipulating diversity. For example, Tilman and Downing (1994) created a diversity gradient in a grassland community by applying different levels of nutrients. Then, they assessed the community resistance and resilience to a strong

drought across this diversity gradient and used statistical techniques to control, as much as possible, the confounding effects of the nutrients.

However, the most direct and powerful assessment of any potential causative agent is through direct manipulations of that agent (Lubchenco and Real 1991). Thus, because diversity may be heavily influenced by many factors, it is critical to use experimental manipulations of diversity to directly attribute cause to it. Because ecology has numerous examples of experimental manipulations of species, although not explicitly manipulating diversity, retrospective reviews of such studies can uncover important patterns (e. g., Risch et al. 1983, Altieri 1994, Allison et al. 1996). To date, however, only a few experiments have directly and explicitly manipulated diversity with the expressed goal of determining effects of diversity (Ewel et al. 1991, Naeem et al. 1994, Tilman et al. 1996).

DISSERTATION RESEARCH

Although these recent experiments mentioned above have demonstrated some important effects of the loss of diversity, we still know little about where to expect diversity effects to be the strongest. The impact that loss of diversity will have on other ecological properties of a system will largely be a function of how the species interactions within a system are modified by the loss. In particular, the magnitude and character of the effects caused by the diversity loss should be determined by the sign of the interaction (positive or negative) and the strength of these interactions. In Chapter 2, I experimentally explore the consequences of loss of diversity to species measures as well

as composite community measures in a high zone, rocky intertidal community. Because the experimental units of this study encompassed a substantial portion of a desiccation gradient, I could also evaluate how strength and sign of interactions varied across the stress gradient.

Much of the theoretical work on diversity/stability relationships has addressed how diversity may modify the effects of a stress as well as the community response to a stress, but little experimental work has been performed in which the diversity has been manipulated. There are notable exceptions (e. g., Tilman and Downing 1994) but the lack of concrete empirical diversity manipulations has left the field with inconclusive evidence of the relationship between diversity and stability. One factor, how diversity may interact with stresses on the community, has rarely been addressed even in theoretical approaches. In Chapter 3, I present results from an experiment in which I tested the "resistance" and "resilience" of an intertidal community subjected to an experimentally-induced thermal stress. This stress created a gradient of heat intensity within each plot which allowed me to assess the magnitude of effects at different stress levels as well as the community recovery from different disturbance levels.

With the advent of "biodiversity" research, the working definition of diversity has broadened but this complexity can confound efforts to pinpoint causation. The potentially important types or "components" of biodiversity have expanded from simple species diversity (richness and evenness) to also include broadly different types of variety such as genetic diversity, functional diversity, ecosystem diversity and phyletic diversity. Even within a group of species it is expected that species number, functional group affiliation and degree of compensation within the group, as well as unique species characteristics

can each play important roles in a community. Our ability to predict the consequences of changes in diversity will be largely dependent on our ability to distinguish the most influential biodiversity "components" within a given system. Further, our ability to generalize among experiments will depend on how comparable experimental results are. In Chapter 4, I evaluate the implications of choice of experimental design in biodiversity research and demonstrate that such choice will have profound implications on the power of detecting different diversity effects. I performed a simulation study in which I tested the power of several experimental designs in detecting known biodiversity effects in simulated "species pools."

The work in this dissertation is part of a field that has dramatically expanded in the past decade. While this field is still grappling with a great number of problems of definition and methodology, the empirical attention already focused on biodiversity topics has transformed historical approaches and uncovered some important patterns. Continuing work in this field promises increased understanding of the ecological consequences of human-induced change of diversity.

CHAPTER 2

Determining the Effects of Loss of Diversity in a Rocky Intertidal Community: The Influence of Sign and Strength of the Affected Species Interactions

ABSTRACT

Predicting where and when loss of diversity will have detrimental ecological consequences will require that we understand how change in diversity modifies species interactions within a community. In particular, the strength and sign of the interactions affected should serve as a guide to the magnitude and direction of the consequences we can expect from changes in diversity. I present results from a diversity experiment in a high zone, rocky intertidal community in which all macroalgal species were manipulated as three groups. Two of the species groups were of relatively high abundance: the fucoids (Fucus spp. and Pelvetiopsis limitata; average about 64% cover), the foliose-reds (Mastocarpus papillatus and Mazzaella (= Iridaea) cornucopiae; average about 30% cover). The third group consisted of all other algal species (≈15 species; mostly of low cover, termed "low abundance species"). I monitored species and community level responses during this 15 month diversity "press" experiment, as well as the recolonization dynamics of excluded species back into reduced-diversity plots. Diversity reduction clearly had important effects at both the species and community levels and these effects were caused by the loss of both strong negative and strong positive interactions. The

primary species-level effect during the experiment was an increase in cover of foliose-red algal species, attributable mostly to competitive release by the removal of the dominant group of algae, the fucoids. Removal of the dominant fucoids was compensated by an increase in canopy cover of the foliose reds, even in a low diversity treatment. However, fucoids in a different low diversity treatment showed the opposite result: biomass was significantly lower in this treatment than in those treatments where other species were also present. Thus, results were highly dependent on the species composition of low diversity treatments. In general, species number was a poor predictor of the change in the community dynamics measured during the press phase. P. limitata recolonized the higher diversity treatment faster than the lower diversity treatment when the diversity press was removed and Fucus spp. showed similar trends. This effect was most likely attributable to higher algal cover and, apparently, the facilitation of P. limitata recruitment by the low abundance species group in the higher diversity treatment. Across a desiccation gradient, interaction strength and sign varied such that diversity effects on community change were greatest under highest stress. Thus, to the degree that species interactions vary with environmental gradients (and other factors), known characteristics of systems such as desiccation potential or temperature stress may serve as a rough guide to where diversity loss will have the strongest effects.

INTRODUCTION

Loss of biodiversity is occurring at unprecedented rates in virtually all types of ecosystems, both through extinction and, more commonly, through local reduction of species richness (Mooney et al. 1995b). While the influence of species diversity on other ecological properties has long interested ecologists (MacArthur 1955, Elton 1958, May 1972, McNaughton 1977, Wolda 1978, Schulze and Mooney 1993a, Mooney et al. 1995a), the recent concern about the widespread loss of diversity has infused the question with an urgency that has driven many investigators to experimentally manipulate diversity (Ewel et al. 1991, Naeem et al. 1994, Tilman and Downing 1994, Tilman et al. 1996). These pioneering studies have demonstrated that species loss can have important ecological consequences such as reduction of productivity (Naeem et al. 1994, Tilman et al. 1996), decreases in nutrient recycling or retention (Ewel et al. 1991, Tilman et al. 1996), and decreases in tolerance and recovery to drought (Tilman and Downing 1994). However, little is understood about where and when diversity loss will have the strongest effects (Lubchenco et al. 1991, Chapin et al. 1995, Risser 1995).

Change in diversity will influence ecological processes and composition primarily by modifying the species interactions in a system. Loss of a species that is the source of a strong interaction will, by definition, yield a strong response in the recipient species, whereas changes in species with weak interaction strengths may have little effect. Thus, knowing the strength of the interactions affected by the change in diversity should tell us something about the overall magnitude of effects (Allison et al. 1996). Further, the effect of one species on another can range from strongly negative (such as a competitive

dominant that excludes the other species) to strongly positive (such as a species that provides a critical nutrient to the other species) (see Callaway (1995) for a review). Although well known examples of positive interactions such as plant/pollinators, coral/zooxanthellae, and plants/mycorrhizae tend to be mutualisms that are mostly obligate relationships, positive and negative interactions are prevalent in all communities and indeed many interactions may be a mix of both positive and negative components (Callaway et al. 1991, Callaway and Walker in press). Further, the sign and degree of interactions may vary with life stages, indirect effects and abiotic stress (Bertness and Callaway 1993, Callaway 1995, Menge 1995).

Understanding the sign of the affected interaction should help us predict the type of change that will occur in other species. Thus, if an interaction affected by species loss is strongly negative, the loss will lead to increased abundance of other species whereas the loss of a strongly positive interaction will lead to the decreased abundance of the remaining species (Figure 2.1A) and the magnitude of these effects is likely to be a function of the strength of the interaction. Loss of a species with no interactions on the remaining species will, by definition, have little effect (Figure 2.1A; middle of the x-axis).

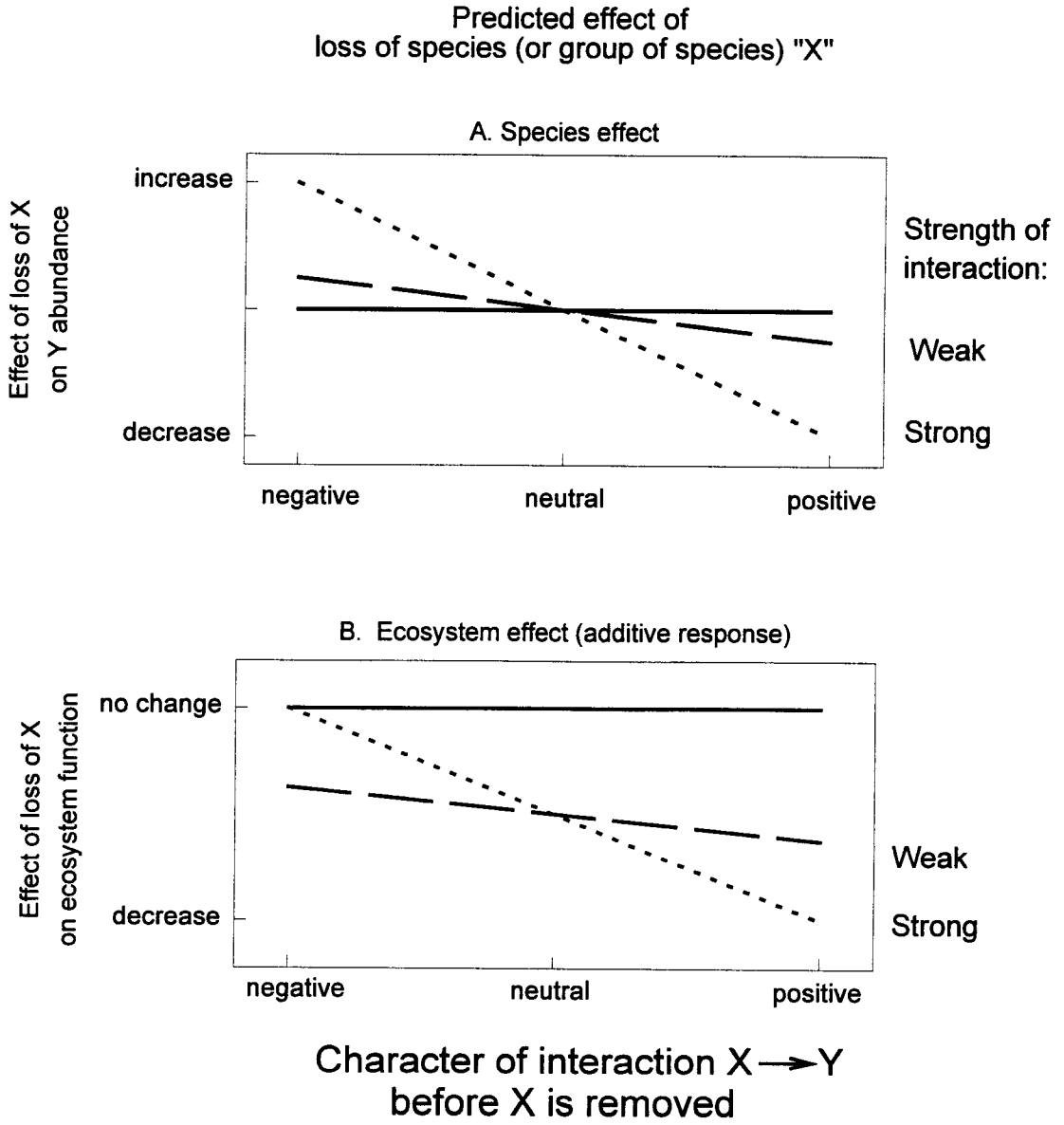

Figure 2.1. Illustration of the effects of strength and sign of species interactions. Graphs show change that occurs with loss of species 'X.' Shown are the changes A) in the abundance of the remaining species, 'Y' and B) in an additive ecosystem measure such as standing biomass. Solid line is a reference indicating no effect of the loss of species 'X,' dashed line indicates weak effects and dotted line indicates strong effects. See text for more explanation.

The loss of such interactions may also influence community dynamics and ecosystem functioning. How such loss will be reflected in these community and ecosystem measures will depend on the nature of the measures. One example of such a measure is standing biomass which is additive of all species responses in a system. In this case, the loss of a strongly negative interaction should be compensated by the increases in abundance of the remaining species (Figure 2.1B; left side of x-axis). Thus, although there is a large change in the species measure, there is little change in the ecosystem measure. Tilman (1996) suggests that this difference between species level and higher level measures accounts for some of the discrepancies within diversity/stability debates. On the other hand, loss of a strongly positive interaction, besides leading to decreased abundance of other species and further loss of diversity, will presumably cause decreases in the functioning of the ecosystem as well (Figure 2.1B; right side of x-axis). Note that because the ecosystem measure discussed here is simply additive, even the loss of non-interacting species (Figure 2.1B; middle of the x-axis) will produce a loss in the ecosystem measure and will be presumably related only to how much the removed species added to the measure (e. g., loss of an abundant species will have a stronger effect on standing biomass than loss of a low abundance species). Thus, given that we know the character of the interactions affected by a species loss, we may predict the consequences of that loss both to remaining species and, potentially, to ecosystem properties. Unfortunately, the current state of knowledge about individual interactions throughout the world's ecosystems is relatively limited (Menge et al. 1994, Chapin et al. 1995, Power et al. 1996).

However, if patterns of positive vs. negative and strong vs. weak interactions are predictable by some known characteristics of communities and ecosystems, then we may be able to generalize this model of species interactions to a rough guide of where loss of diversity may have stronger effects. For example, if we know the conditions under which competition among species that share an ecosystem functional role is likely to be stronger, then we would predict that loss of species under those conditions is less likely to produce an ecosystem change than under conditions where there are many positive or even neutral interactions among the species.

Some important broad predictions have been made about how the strength and sign of interactions vary. Menge and Sutherland (1987) predicted that the strength of interactions will vary with physical stress and other external factors: that in communities dominated by strong physical stress or low recruitment, competition will be low. In such cases the interactions among species will be weaker than under more benign physical conditions and higher recruitment. Bertness and Callaway (1993) predicted that positive interactions will be more prevalent under conditions of harsh physical stress or strong consumer pressure. For example, it has been demonstrated that positive interactions are more common in areas of high physical stress where "neighbor" effects ameliorate stress, but are less common in physically more benign areas where competition becomes more important (Bertness and Hacker 1994, Callaway 1995, Bertness and Leonard in press). If such patterns are widespread, then we may be able to use such broad predictions as a guide to factors that will influence the effects of diversity loss.

One factor that may complicate the predictive power of this rough guide is the distribution of interaction strengths within a community; not all species have the same

community impact. For systems in which a small number of species have a disproportionately strong effect on the community (that is, the distribution of species interaction magnitudes is strongly skewed (Power et al. 1996)), the diversity of a system may be a poor predictor of the changes in it and it will be critical to identify those strong interactors (Paine 1966, 1980, Menge et al. 1994, Chapin et al. 1995, Estes and Duggins 1995, Allison et al. 1996, Navarrete and Menge 1996, Power et al. 1996). In other cases, there may be multiple species with profoundly strong effects, but the remaining species can compensate for the loss of some species (Menge et al. 1986). Thus, to evaluate the usefulness of this rough guide to diversity effects requires that we evaluate the strength, sign and distribution of interactions within a community.

However, surveying an entire community for such characteristics can be an extremely complex endeavor because there are numerous potential species-to-species interactions to explore. One way to make a first approximation is to manipulate groups of species involving many or most of the species in a community (e. g., Menge and Lubchenco 1981, Menge et al. 1986). Although manipulating whole sets of species at a time will not allow us to attribute effects to a specific species, it does two important things. First, it identifies where the stronger effects may be. For example, lumping species by some functional characteristic, such as feeding mode (predators/herbivores), morphology (canopy/understory species) or physiology (C3/C4 plants), should allow us to quickly determine which groups participate strongly in a tested response. Second, lumping allows us to manipulate a large number of less abundant species and to determine relatively quickly if there are strong interactors not apparent by their abundance within the group. Under such a scheme, if we find that all groups have an

impact on response variables that is not compensated for by other groups, then the diversity represented by the differences in the groups is important in the system. If one group is particularly important and the others less so, the results suggest that the identity of the diversity change is critical and we can then focus on those species in the group with strong effects. If none of the groups have particularly strong effects, the results imply that the interactions within the system are influenced by external factors and that changes in diversity will not necessarily be a good predictor of other ecological properties.

In this paper, I present the results of an assessment of the effects of changes in the diversity of a dominant group of species on the dynamics of a community. In a diversity-reduction experiment performed in a rocky-intertidal community, I manipulated the diversity of macroalgae (the dominant biomass) and measured the influence of diversity treatments on community dynamics. Specific responses involved measuring the adjustment of the remaining dominant species and community measures to the diversity press, and the species recolonization patterns in exclusion plots. The species manipulated were lumped into three groups — two groups, each consisting of two common species, and expected to have stronger effects if effects are a function of abundance, and the third consisting of all other, mostly low abundance species (≈15 species), and expected to be important in cases where species number is important. By manipulating combinations of these groups, I created a gradient of diversity treatments, from low to medium to high. This allowed assessment of how diversity, measured both as the number of species groups and as the number of species, influenced community dynamics.

The community in which the experiment was performed, the high rocky intertidal, is particularly susceptible to desiccation stress. In other rocky intertidal studies, a prevalence of positive interactions (both intra- and inter-specific) due to this high stress has been demonstrated in a few systems (Bertness 1989, Bertness and Hacker 1994, Bertness and Leonard in press). Within this experiment, there was a gradient of desiccation potential that allowed me to evaluate if interactions vary over this physical gradient and how loss of diversity might influence such effects.

The specific questions I address with this experiment and analysis were: (1) How do species and community measures adjust to the reduction of natural diversity? (2) What are the community characteristics of reduced diversity treatments? (3) Does diversity of a community influence natural recolonization into that community? And (4) do positive interactions play a role in the dynamics of this system?

SYSTEM DESCRIPTION

This study was performed in the intertidal high zone of the rocky benches at Fogarty Creek Point (44° 51' N, 124° 03' W) just south of Fogarty Creek State Park, on the central coast of Oregon, USA. Several aspects of this site have been described (Farrell 1989, 1991, Blanchette 1994, Berlow 1995, Navarrete 1996). The low zone of this site is composed of a mosaic of kelps, seagrass and urchins and the mid zone is dominated by beds of the mussel Mytilus californianus. The high zone is dominated by macroalgae (mostly the fucoid species, Fucus gardneri and Pelvetiopsis limitata, and

foliose red species, Mastocarpus papillatus and Mazzaella cornucopiae) and acorn barnacles (mostly Balanus glandula and Chthamalus dalli). The experiment was performed across an extensive portion of the site in areas where the exposure to wave energy ranged from moderately protected to moderately exposed. The terrain within this area was complex such that there was often substantial variation of substratum angle within a 1 m^2 plot. Compared to other sites on the central Oregon coast, Fogarty Creek in this zone had a high degree of algal diversity at the scale of the 1 m^2 experimental plots (G. Allison, personal observation).

High intertidal zone and physical stress

The high intertidal zone of rocky shores is characterized by short immersion times that occur only during high tides of sufficient magnitude. For the mixed semi-diurnal tides of the Northeastern Pacific, the timing of tidal excursions is such that during some seasons, water may cover high intertidal zones only once per day (NOAA 1993, G. Allison, unpublished data). In Oregon, the potential desiccation stress of infrequent immersion can be amplified by other conditions such as high winds or high temperatures and calm wave conditions (thus reducing the effective height that water reaches during high tide) in late spring through early fall. Upper range limits in the rocky intertidal are often determined by physiological tolerance to desiccating conditions (Connell 1961, Schonbeck and Norton 1978, Lubchenco 1980, Davison et al. 1993, Davison and Pearson 1996) and the upper edge of this zone was the upper limit of the tidal range of many species. In the experiment described below, the upper limit of several species even

occurred within the range of tidal heights encompassed by the plots. For example, the species Nucella emarginata (a whelk) and Semibalanus cariosus (a barnacle), abundant in lower zones and often playing ecological critical roles, only occurred in low densities in this experiment, and then, only in the lowest of the plots.

Some factors can modify this potential stress. For example, some species occur predominantly on north-facing slopes of the substratum (G. Allison, unpublished data, Olson 1985). Further, an algal canopy can ameliorate some of the desiccation stress (Dayton 1975, Menge 1978a, b) by holding in moisture, reducing temperature and providing some shelter from winds.

Focal species

To create a diversity gradient, I divided all macroalgae (listed in Table 2.1) into three groups. The first group consisted of the fucoid brown algal species (F. Fucaceae, O. Fucales): mostly Fucus gardneri and Pelvetiopsis limitata but some Fucus spiralis occurred in the most wave protected areas. Plant morphology within this group can be very plastic and plant size in F. gardneri is inversely proportional to wave exposure (Blanchette 1994). In this zone, the mean length of F. gardneri was 8.2 cm (N=58, std. dev. = 4.2 cm; measured in May 1994 in control plots from each block) and the mean length of P. limitata was 6.0 cm (N=49, std. dev. = 1.8 cm). P. limitata typically occurs higher on the shore than F. gardneri. Although at some sites along the Oregon coast these species have separate tidal distributions, they overlap extensively at Fogarty Creek. The average cover for this group of species was approximately 64%.

The second group were the common red foliose (O. Gigartinales) species: Mastocarpus papillatus and Mazzaella (=Iridaea) cornucopiae (see Hommersand et al. (1994) for reclassification information). Both of these species are abundant in the high intertidal zone of the Pacific Northwest of the USA (Gabrielson et al. 1990). These red algae both develop from fleshy crusts into a compact aggregation of blades (Abbott and Hollenberg 1976, Gabrielson et al. 1990). M. cornucopiae blades typically grow to 2-4 cm tall and stand erect from their holdfast. Mature blades of M. papillatus can reach 15 cm in length (Abbott and Hollenberg 1976) but maximum size from a census of 50 random plants in this study was 10 cm. When the blades are shorter, they stand erect, but as they grow longer they lie on the substratum at low tide creating a canopy around the holdfast. The turf/crust morphology of these species allows them to persist through heavy grazing and physical stresses (Hay 1981). The average cover for this group of species was approximately 30%.

Experimental group	Species	Algal Division	Max. cover in 625cm^2 subsample	Mean cover	Std. Dev.
Fucoid species	Fucus spp.	Phaeophyta	1.000	0.392	0.252
	Pelvetiopsis limitata	Phaeophyta	0.968	0.245	0.235
Foliose red species	Mazzaella (=Iridaea) cornucopiae	Rhodophyta	0.953	0.157	0.200
	Mastocarpus papillatus	Rhodophyta	0.875	0.137	0.167
Low abundance species	Endocladia muricata	Rhodophyta	0.781	0.095	0.120
	Cladophora columbiana	Chlorophyta	0.609	0.062	0.103
	Odonthalia floccasa	Rhodophyta	0.313	0.0025	0.0183
	Analipus japonicus	Phaeophyta	0.0156	0.0024	0.0056
	Porphyra spp.	Rhodophyta	0.0781	0.0014	0.0057
	Scytosiphon lomentaria	Phaeophyta	0.0938	0.0013	0.0063
	Neorhodomela larix	Rhodophyta	0.125	0.0012	0.0079
	polysiphonous red spp.	Rhodophyta	0.0469	0.0010	0.0049
	Leathesia difformis	Phaeophyta	0.0625	0.00094	0.0052
	Mazzaella (=Iridaea) splendens	Rhodophyta	0.0343	0.00049	0.003
	Petalonia fascia	Phaeophyta	0.0156	0.00023	0.00187
	erect coralline spp.	Rhodophyta	0.0156	0.00013	0.0014
	Ulva spp.	Chlorophyta	0.0156	0.00013	0.0014
	Callithamnion pikeanum	Rhodophyta	0.0156	0.00007	0.0010
	Prionitis spp.	Rhodophyta	0	0	0
	Blidingia minima	Chlorophyta	0	0	0
	Halosaccion glandiforme	Rhodophyta	0	0	0

Table 2.1. Algal species list and abundance. Mean, standard deviation and maximum cover was calculated from all (625 cm^2) subsamples and from four census dates in 1993/94 measured in 15 1m^2 unmanipulated plots. Maximum cover calculated from subsamples from all plots in July 1993. Species shown with mean of zero occurred in other treatments, although at low abundance (< 3%). Species are ordered by mean abundance.

The third group consisted of all other macroalgal species and are listed in Table 2.1. The two most common species in this group were Endocladia muricata and Cladophora columbiana. E. muricata (O. Gigartinales) is a perennial red alga, with dense bushy thalli that can form thick mats (Glynn 1965) but more commonly, in the experimental plots, were patchily distributed. C. columbiana is a green filamentous alga that forms low dense mats. Cover of C. columbiana is relatively seasonal with the highest cover in late spring and summer. Its dense mat morphology acts like a sponge and can hold a large amount of water. Other species in this group, although occasionally present in a substantial portion of one or a few subplots, had mean covers of less than 1%.

Other species that occurred in the experimental plots included the barnacles Balanus glandula, Chthamalus dalli, limpets Lottia digitalis, L. pelta and L. strigatella, herbivorous snails Littorina spp., and occasionally, the predatory snail Nucella emarginata. Birds observed to feed on organisms in the plots were the western gull Larus occidentalis, the black oystercatcher Haematopus bachmani, the black turnstone Arenaria melanocephala, the surfbird Aphriza virgata, and the American crow Corvus brachyrhynchos (see Marsh 1986). Throughout the remainder of this and subsequent chapters, all species are referred to by their generic names, except for multi-species genera.

METHODS

Experiment description

Ten plots, 1 m^2 in area, initially of high algal diversity, were randomly assigned to each of several treatments in a randomized block design. Different diversity treatments were created by removing different numbers (0, 1 or 2) of these algal groups (Table 2.2). A fully factorial design (all combinations of the presence and absence of the three groups) was not possible because of limited area for adequate replication.

I performed the initial removal of excluded species in April and May 1993. I controlled for the amount of bare space created in the low diversity plots in initial removals by creating the same amount of bare space in all treatments. I did this by first calculating the change in bare space for all plots (initial post-weeding cover minus pre-weeding cover) and then using these numbers to determine how much more bare space to add to a plot. I added bare space in 25 cm^2 squares randomly assigned throughout the 1 m^2 plot. This creation of bare space effectively served as a calibrated disturbance to all treatments.

Diversity treatment Code	Reduced treatment code	Diversity treatment level	Algal groups manipulated: Fucoids	Foliose reds	Low abundance species	Average species richness (SE)
H: +F+R+M	H	high	+	+	+	27.4 (1.81)
M1: -F+R+M	M1	moderate	–	+	+	24.3 (2.00)
M2: +F+R-M	M2	moderate	+	+	–	18.9 (0.43)
L1: +F-R-M	L1	low	+	–	–	15.0 (1.02)
L2: -F+R-M	L2	low	–	+	–	13.3 (0.75)

Table 2.2. Treatment structure and diversity within treatments. All macroalgal species were lumped into one of the three groups: fucoids = Fucus spp. and Pelvetiopsis limitata; foliose reds = Mastocarpus papillatus, Mazzaella (=Iridaea) cornucopiae; low abundance species = all other macroalgal species including Endocladia muricata and Cladophora columbiana (see Table 2.1 for a complete list). '+' = group included in the treatment, '–' = group excluded from the treatment. Average species richness per plot throughout diversity press phase includes all macro-flora and fauna except very small or highly mobile species. SE = standard error of species richness. Throughout this paper, either the full code (e. g., "L1:+F-R-M") or the reduced codes are used to refer to the diversity treatments. In the full codes, "F" refers to fucoid, "R" to foliose reds and "M" to low abundance species group.

Subsequently, during the diversity press phase, "weeding" was performed by carefully removing all recruits of the excluded species. Individual recruits were removed from the plots either manually or by knife-point to avoid disturbing non-excluded species. Although this was a time consuming procedure, the amount of low-tide time available in this zone allowed every plot to be completely weeded approximately every two weeks.

The diversity treatments were maintained for 15 months, until August 1994, after which natural recolonization of excluded species was allowed to occur.

The experiment was divided into two phases, "press" and "recolonization." In the press phase, the response variables included both species and community responses. Species responses were the changes in the species remaining in the plots. The species responses I report for this phase are the cover of Fucus, Pelvetiopsis, Mastocarpus and Mazzaella. Only those treatments with those species present were included in the analysis. Analyses for the "low abundance" species group are not presented; there were only two treatments from which this group was not excluded (H and M1) and these treatments were not statistically different for these species. Community responses reported in this paper are 1) total algal cover, or the sum of the cover of all algal species (and, because of layering, can be greater than 100%), 2) canopy cover (the fraction of a censused plot covered by at least one algal species) and 3) total standing algal biomass. Because algal layering was extensive in this community (in some cases, as many as six species occupied a single grid point, projected vertically), total algal cover was a better representation of community complexity than was canopy cover. On the other hand, canopy cover best represented the character of the algal community likely to be important for desiccation stress and space occupancy.

The recolonization phase began with the cessation of the diversity press when all excluded species were allowed to naturally recolonize the plots. Species responses of Fucus, Pelvetiopsis, Endocladia and Cladophora were quantified. Because I was interested in the recolonization of species into the reduced diversity treatments, I only compared treatments from which the species had been excluded during the diversity

press. Because Mastocarpus and Mazzaella were only excluded in one treatment (L1), they were not included in these analyses.

Spatially explicit data collection

Cover data were collected in a spatially explicit manner in two 0.25 m^2 subplots within each 1 m^2 plot using grids of 256 (16x16) uniformly spaced points (Figure 2.2). Raw data consisted of all species intersecting each grid point. Hence, these data document vertical layering, and estimated abundance at levels of canopy, understory species, and the substrate occupiers. From the raw data, I calculated percent cover estimates and point and plot diversity measures. The data also delineate the patch structure for various algal species, and suggest some spatial relationships between species. Registration of this grid over the same subplot from one census to the next was precise enough to follow patches or organisms that intersected at least 4 grid points (about 40 cm^2). Smaller organisms intersected by fewer grid points (e. g., small plants or individual barnacles) could not be reliably followed through time in a spatially explicit manner. Although this level of resolution was fairly precise, because the position of an alga on the substratum was dependent on the most recent wave direction for most algal species, spatial patterns were nonetheless not highly repeatable even from one low tide to the next. Therefore, the spatial aspect of these data was used mostly to generate spatial descriptions such as patch size for a given census date.

Throughout the diversity press, data were also taken in 4 subsamples (625 cm^2) of each 0.25 m^2 subplots on total species richness and, densities of limpets (larger than 0.4

cm) and Nucella. Littorines were very abundant in virtually all plots and were not counted. Both aspects of these censuses (grid survey and richness/limpet counts) were performed only during non-desiccating conditions because desiccation reduced plant size and therefore total cover and substantially reduced the activity of mobile species (and hence my ability to detect them). Further, because weather conditions sometimes prevented sampling, some censuses took as long as 6 weeks to perform. To reduce potential biases induced by the time lag between the first and last plots censused, I monitored on a block-by-block basis rather than a treatment-by-treatment basis.

During the press portion of the experiment, each treatment consisted of 10 replicate plots, with 2 plots of each per block. At the start of the recolonization phase, only one plot from each block was used in each treatment (the second plot was used in a different experiment, see Chapter 3). When appropriate, I use all ten replicates to report on treatment differences during the press phase. However, I use only the subset of plots that were directly involved in the second phase to follow recolonization dynamics.

Taking data in a spatially explicit manner allowed me to further subdivide sample units for other purposes. For instance, to explore the relationships between the physical correlates of desiccation stress and community dynamics, I subdivided the 0.25 m^2 subplots into four "sub-subplots" because physical correlates such as substratum angle and tidal height often varied greatly, even over this small area. I therefore took measurements for some of the physical variables at the sub-subplot scale.

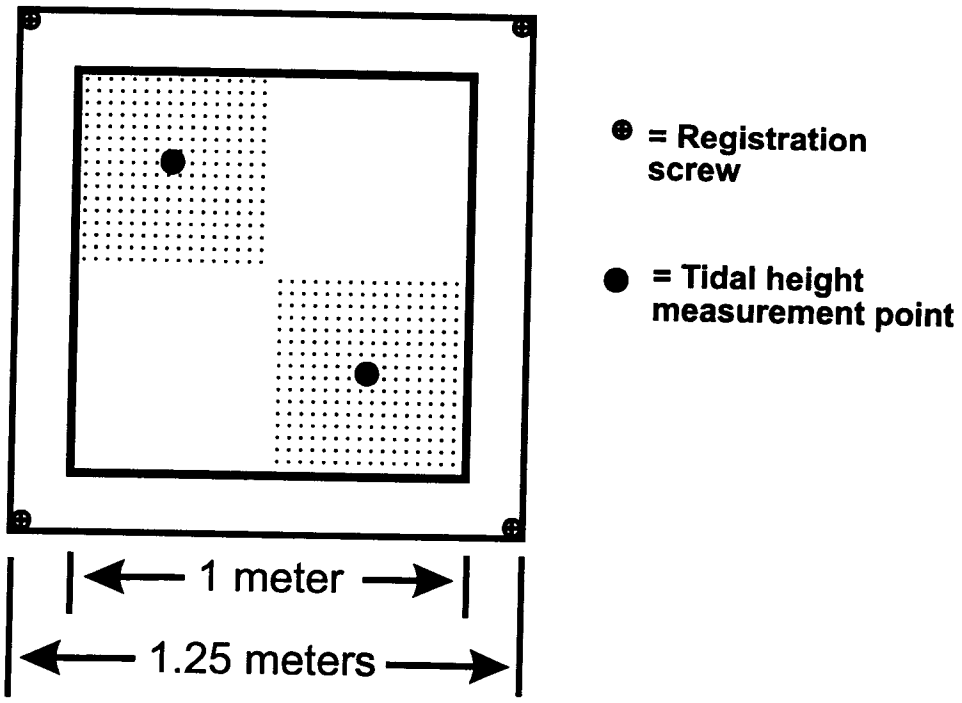

Figure 2.2. Layout of experimental plots. Outside square indicates the area of each plot that received the diversity treatment (species exclusions and bare rock compensation). The inner square indicates the sampling area. Each plot had two $0.25m^2$ sampled areas (in opposite corners but selected at random) that consisted of a grid of 256 uniform points. Successive censuses registered each subplot by attaching the quadrat to all registration screws. Also indicated are the points used to estimate relative emersion index.

Biomass calculation

Standing algal biomass was calculated using an equation generated by a regression of canopy cover and the cover of some dominant species. This regression equation was developed by censusing 28 quadrats at Fogarty Creek. Quadrats were chosen to span the range of algal cover and species mixes found in the experimental plots. After each quadrat was censused, all algae were removed from the quadrat, returned to the lab, cleaned of epifauna, dried of excess moisture with a lettuce spinner, and wet

weighed. The algal samples were then dried to constant mass and weighed again. Regression equations were developed using stepwise linear regression. Canopy cover, the cover of each dominant individual species and the cover of groups of species were all used as potential factors in the regression model. The model intercept was forced through zero. The equation for wet biomass was:

$$\text{Standing wet algal BIOMASS (grams/0.25 m}^2\text{)} = 431.0*(\text{CANOPY}) + 545.7*(\text{FUCOID})$$

(model $p<0.0001$; $R^2 = 0.869$; R^2 for the model with an intercept included was 0.634) where CANOPY and FUCOID are proportional cover of all algae and fucoid plants, respectively. The equation for dry biomass was:

$$\text{Standing dry algal BIOMASS (grams/0.25 m}^2\text{)} = \text{CANOPY}*232.5$$

(model $p<0.0001$; $R^2 = 0.916$; R^2 for the model with an intercept estimated was 0.642). Because this measure of standing dry algal biomass is linearly related to canopy cover, and therefore, would produce the same results in statistical analyses and the same patterns in graphical illustrations, I will not report it throughout the rest of the paper.

Data Analysis

Most statistical tests were performed using repeated-measures analysis to check both the treatment effects (hereafter termed TRT) and the time-by-treatment (TIMExTRT) interaction. I checked assumptions of normality with normal probability plots and the Shapiro-Wilk statistic (SAS Institute Inc. 1988) and I checked homogeneity of variance with residual plots. I used arcsin-squareroot or log transformations when

these assumptions were not met. In all cases, transformations succeeded and are indicated in the results tables.

Because I was interested in the simultaneous responses of several species as well as responses of several community measures to the treatments, a multivariate approach was the most appropriate method of analysis. Multivariate analysis reduces multiple tests and accounts for the correlation structure among dependent variables (Scheiner 1993). Furthermore, because I was interested in the dynamics of these response variables over several census dates, a repeated-measures analysis was appropriate. Therefore, for the diversity press data, repeated measures multivariate analysis of variance (RM-MANOVA) was used (SAS Institute Inc. 1989, chapter 24 and von Ende 1993). This type of analysis accounts for multiple measures on several, potentially correlated, response variables. However, although a single full model that included all levels of all treatments and all response variables may have been ideal to account for the correlation structure (Scheiner 1993, von Ende 1993), this was not possible. Not all treatments could be used for all species because some were explicitly manipulated by the experiment. For example, including treatments involving fucoid removal would have been inappropriate for the analysis of Fucus. Therefore, as a compromise between fully multivariate (inappropriate because of experimental design) and fully univariate (inappropriate because of correlation among dependent variables), I performed separate RM-MANOVAs on three groups of variables (i. e., fucoids, foliose reds, community variables). In each of these analyses, pre-planned contrasts were performed to test the effect of each group of manipulated algae on TRT or TIMExTRT effects and are reported when these effects are significant. The analysis models also included block effects

(hereafter termed BLK). For the diversity press analysis, because there were two sample units per block in each treatment, the BLKxTRT interaction was used as the error term to test for TRT effects (Potvin 1993).

For the recolonization dynamics, there were not adequate degrees of freedom to perform the RM-MANOVA. I, thus, used repeated-measures analysis on single species responses as outlined by von Ende (1993). I used Mauchly's sphericity test (Littell et al. 1991) to verify the assumptions of the univariate form of repeated measures tests. In all appropriate cases (number of treatments > 2), the hypotheses of sphericity were rejected, implying that the univariate form of repeated measures may inflate significance. The MANOVA form of the test is not sensitive to deviations from sphericity but is less powerful than the univariate form (SAS Institute Inc. 1989, von Ende 1993). I present results from both forms of the tests.

Desiccation potential analysis

In the analysis of the effect of desiccation on community dynamics, I performed a regression analysis of two measures of desiccation potential, emersion time and substratum angle, on measured dynamics. Because shore topography at Fogarty Creek was heterogeneous, and the wetting of the high intertidal was highly influenced by wave splash, absolute tidal height within the zone of my experiment was a poor measure of the amount of time a plot was wetted by waves each day. Therefore, I developed a more direct measure I term "relative emersion index." This measure was determined by observing the time (with a resolution of 10 minutes) that incoming tides wetted and

finally covered two points in every plot (Figure 2.2) on ten separate days when waves were small. These measures were then used to calculate an "effective" tidal height from the predicted tidal heights of those days (NOAA 1993), and the ten values averaged to yield a mean effective tidal height for the two points in every plot. The ranking of the relative emersion times of these points was verified by numerous spot checks throughout the course of the experiment. Although this index was not representative of all wave conditions, it was useful for characterizing the conditions most likely to be desiccating: calm conditions which usually occur in late spring and summer.

The north/south angle of the substratum is a measure of the degree of exposure to the sun. Because experimental plots could be highly heterogeneous for this character, the north/south component of this angle was measured in eight places in every plot. Because it was expected that the most desiccating angle would be that angle perpendicular to the sun's rays at midday in the summer, the measures were transformed so that the maximum value corresponded to the greatest desiccating angle and zero to the greatest angle away from the perpendicular. For the regression analysis, both substratum angle and relative emersion index were normalized so values ranged from zero to one, with zero being the measure of the least potential desiccation and one being the most. For the regressions, I used the eight subsamples within each plot. Each subsample had a unique measure of the relative emersion index and substratum angle. The analyses tested for the presence of significant regressions within each of the diversity treatments.

Data were analyzed using SAS (version 6.04 for DOS) for IBM-compatible personal computers (SAS Institute Inc. 1989). Spatially explicit data were managed with a set of Pascal programs written specifically for this data set that could produce summary

statistics at various scales within an experimental plot or for individual patches within a plot.

RESULTS

Diversity press phase

Diversity treatment effects varied with the species of interest. There was a significant TRT effect on the foliose red group. This treatment effect was attributable mostly to the presence or absence of fucoids (see contrasts, Table 2.3A) although there was a trend of an effect of the low abundance species group ($p=0.0945$). There was also suggestion that this treatment effect varied over time (Table 2.3A; TIMExTRT, $p=0.0754$), again apparently attributable to the fucoids.

Although diversity reduction had no overall effect on the fucoids (Table 2.3B; RM-MANOVA, neither TRT nor TRTxBLK effects were significant), rates of change of fucoids did vary through time with both TRT and BLK (within subjects TIMExTRTxBLK was significant). Also, the significant effects of BLK implied that this trend varied in space. Although the effect was weak, rates of change of fucoids tended to be slower in the lowest diversity treatment (Figure 2.3A,B). Note that the lower rates in the fucoid-only treatment (L1) suggests that interactions with other groups (probably the foliose reds) were positive.

Table 2.3. RM-MANOVA results for the dynamics during the diversity press for cover of major algal species. Species in each group: A) Mastocarpus and Mazzaella, B) Fucus and Pelvetiopsis. All algal cover was first arcsin-squareroot transformed. Dates included in TIME were July 1993, October 1993, March 1994 and August 1994. Treatments examined were only those in which the analyzed species was included during the diversity press (A= H, M2, L1; B=H, M1, M2, L2). Ten plots used per treatment. Reported are the Wilks' lambda statistic, numerator degrees of freedom (num df), denominator degrees of freedom (den df), and the standard F and P values for the hypothesis of no effect of the source of variation. Results of preplanned contrasts of the effects of TRT and TIMExTRT effects are shown if those main effects are significant. '*' indicates that although the TIMExTRT effect is marginally non-significant, contrast results are also shown. P-values in bold are significant at the $\alpha = 0.05$ level.

A. Foliose reds

BETWEEN SUBJECTS

SOURCE	Wilks' λ	num df	den df	F	P
TRT	0.149	6	22	5.84	**0.0009**
BLK	0.254	8	38	4.67	**0.0005**
TRT x BLK	0.0328	24	38	1.18	0.3170
TRT Contrasts:					
FUCOIDS	0.250	2	11	16.5	**0.0005**
LOW ABUNDANCE SPECIES	0.651	2	11	2.95	0.0945

WITHIN SUBJECTS

SOURCE	Wilks' λ	num df	den df	F	P
TIME	0.057	6	15	41.3	**0.0001**
TIME x TRT	0.058	18	20.2	1.94	0.0754*
TIME x BLK	0.089	24	53.5	2.23	**0.0076**
TIME x TRT x BLK	0.036	72	87.4	1.02	0.4605
TIME x TRT Contrasts:					
FUCOIDS	0.188	6	7	5.00	**0.0264***
LOW ABUNDANCE SPECIES	0.720	6	7	0.452	0.8232

Table 2.3 (continued)

B. Fucoids

BETWEEN SUBJECTS

SOURCE	Wilks' λ	num df	den df	F	P
TRT	0.576	4	14	1.11	0.3901
BLK	0.155	8	28	5.38	**0.0004**
TRT x BLK	0.320	16	28	1.34	0.2396

WITHIN SUBJECTS

SOURCE	Wilks' λ	num df	den df	F	P
TIME	0.114	6	10	13.0	**0.0003**
TIME x TRT	0.097	12	6	1.11	0.4762
TIME x BLK	0.014	24	36.1	3.60	**0.0003**
TIME x TRT x BLK	0.0078	48	53.3	1.86	**0.0139**

Thus, at the species level, the fucoid effect on Mastocarpus and Mazzaella was the strongest effect of the diversity reduction. In –fucoid treatments, Mastocarpus and Mazzaella cover increased substantially compared to the +fucoid treatments (Figure 2.3C,D), and increases of Mastocarpus were the largest. Although cover of Mastocarpus increased in all treatments (Figure 2.4) including non-manipulated controls (not shown), increases were much greater in the fucoid exclusion treatments (treatments M1, L2). Many plots in these treatments were characterized by the development of large patches of Mastocarpus (Figure 2.5), usually in the same areas from which the fucoids had been removed. Thus, the sign of the interactions with removed groups on the foliose reds was negative.

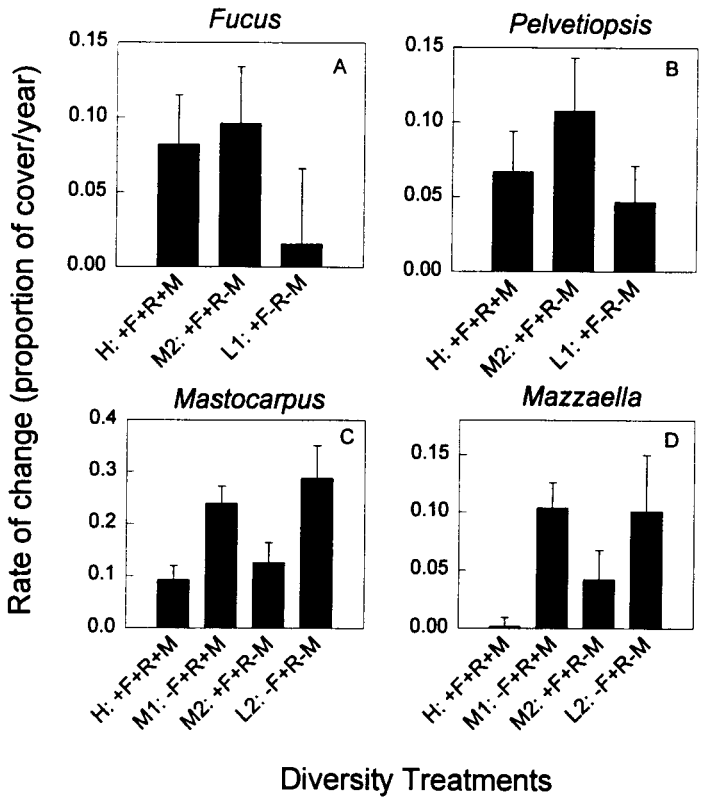

Figure 2.3. Rates of change during diversity press: species measures. Rates calculated as the slope of the regression of abundance over time in the diversity press phase. See Table 2.3 for analysis. Error bars are standard errors. Ten plots used per treatment. Treatments are arranged by descending diversity.

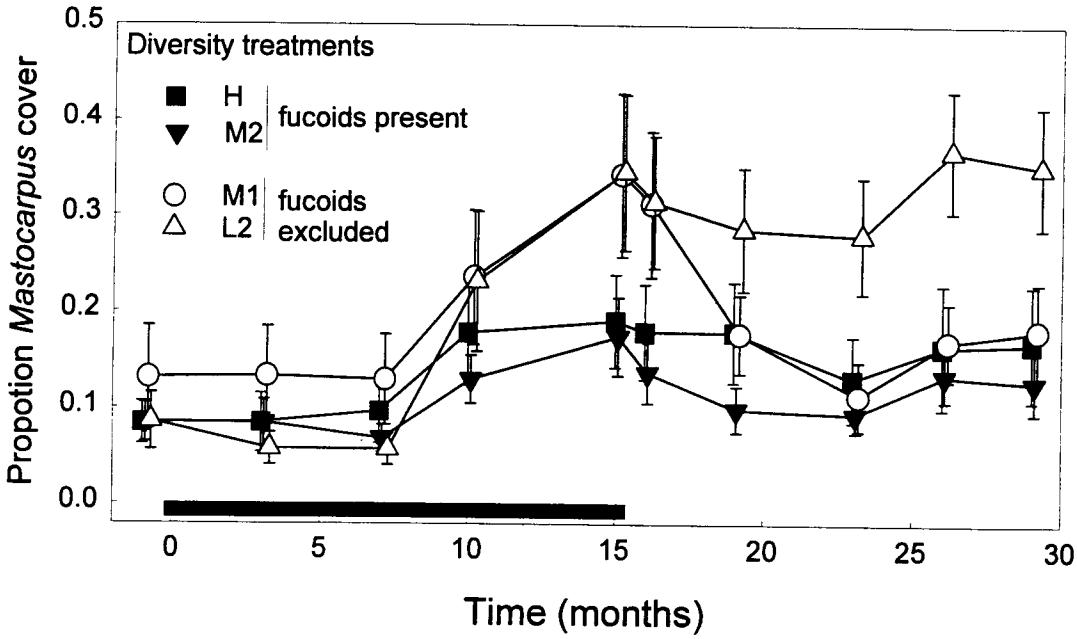

Figure 2.4. Mastocarpus cover during experiment for the three reduced diversity treatments. Only those plots used throughout the experiment are shown (n=5/treatment). Error bars are standard errors. The heavy line on the x-axis indicates the diversity press phase of the experiment.

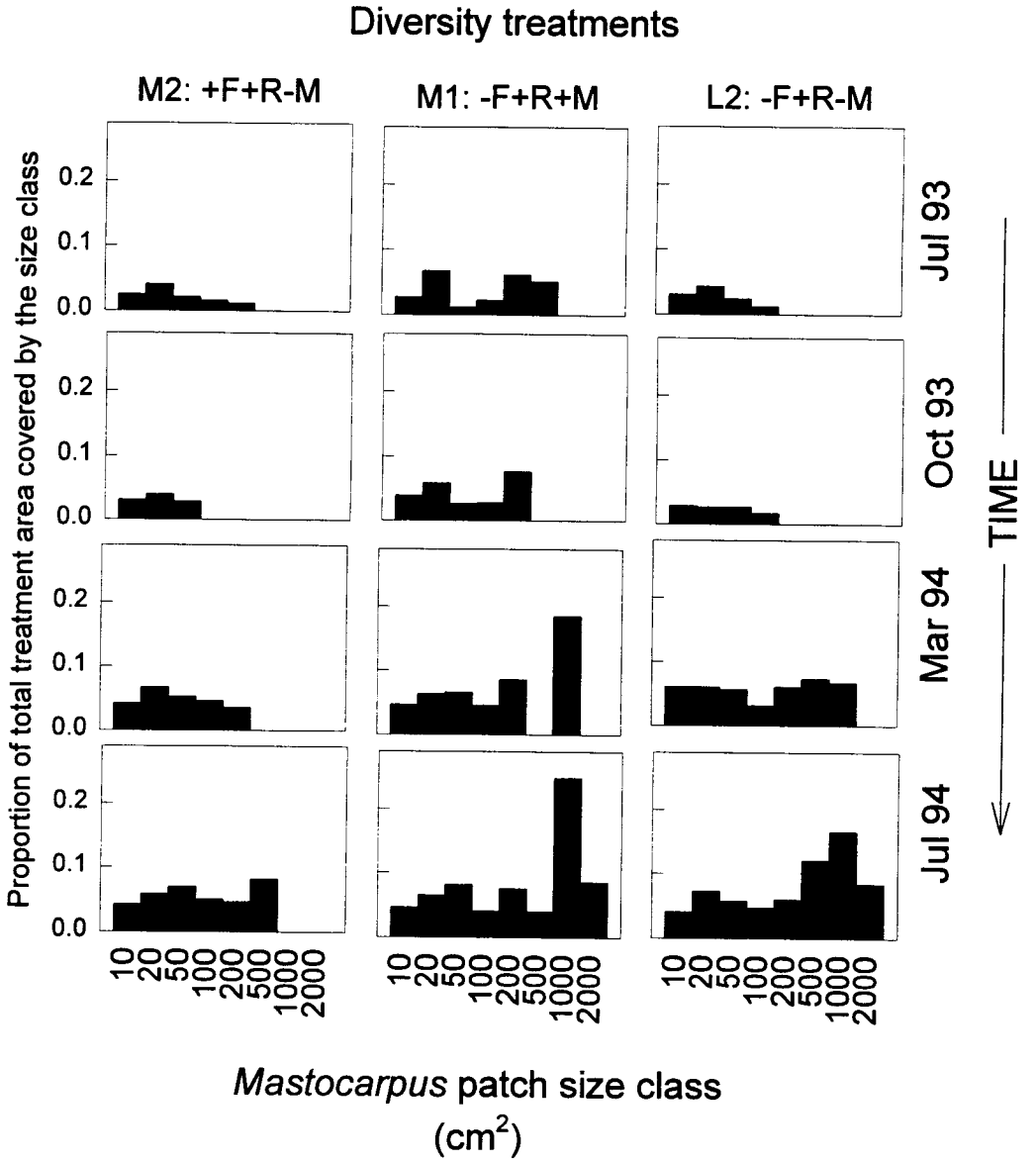

Figure 2.5. Size distribution of Mastocarpus patches in three treatments throughout the press phase of the experiment.

At the community level, diversity reduction had strong effects (Table 2.4; all effects but TIMExBLK were significant). Further, all three manipulated algal groups had an influence on the dynamics (Table 2.4; TRT and TIMExTRT contrasts). Patterns of change for specific community measures (Figure 2.6) reflected changes that occurred at the species level: canopy cover increases were fastest in the two –fucoid treatments (M1, L2) and the slowest response was in the low diversity treatment (L1: +F-R-M). The dominant pattern of change for total algal cover was simply very low rates in this latter low diversity treatment. Biomass changed fastest in the two higher diversity, +fucoid treatments (H, M1). This was expected because standing wet algal biomass was heavily influenced by the abundance of fucoids (see equation, Biomass calculation section). The relatively high rates of increase in –fucoid treatments was due presumably to release from competition with the fucoids of Mastocarpus and Mazzaella. However, the lower biomass rate for the low diversity, +fucoid treatment (L1) was due to low rates of both Fucus and Pelvetiopsis in that treatment (Figure 2.3).

Thus, the most conspicuous effects in the diversity press phase were 1) the effect of fucoid-removal on Mastocarpus and Mazzaella that was also reflected in canopy cover and 2) the lower rates of recovery in Fucus in the +fucoid low diversity. This latter effect was more evident in the biomass, canopy and total algal cover of that treatment than in the species measures.

Table 2.4. RM-MANOVA results for the dynamics during the diversity press for community measures. Dependent variables in the model were total algal cover, canopy cover and standing algal biomass (wet). Canopy cover was arcsin-squareroot transformed and wet biomass was log transformed. See Table 2.3 for further details.

Community variables

BETWEEN SUBJECTS

SOURCE	Wilks' λ	num df	den df	F	P
TRT	0.011	12	37.3	14.3	**0.0001**
BLK	0.239	12	61.1	3.66	**0.0004**
TRT x BLK	0.0873	48	69.2	1.83	**0.0106**
TRT Contrasts:					
FUCOIDS	0.051	3	14	86.8	**0.0001**
FOLIOSE REDS	0.196	3	14	19.4	**0.0001**
LOW ABUNDANCE SPECIES	0.396	3	14	7.13	**0.0039**

WITHIN SUBJECTS

SOURCE	Wilks' λ	num df	den df	F	P
TIME	0.060	9	17	29.6	**0.0001**
TIME x TRT	0.012	36	31.7	2.00	**0.0255**
TIME x BLK	0.101	36	65.4	1.53	0.0652
TIME x TRT x BLK	0.0006	144	150	1.63	**0.0016**
TIME x TRT Contrasts:					
FUCOIDS	0.188	9	8	3.83	**0.0360**
FOLIOSE REDS	0.121	9	8	6.43	**0.0077**
LOW ABUNDANCE SPECIES	0.181	9	8	4.02	**0.0314**

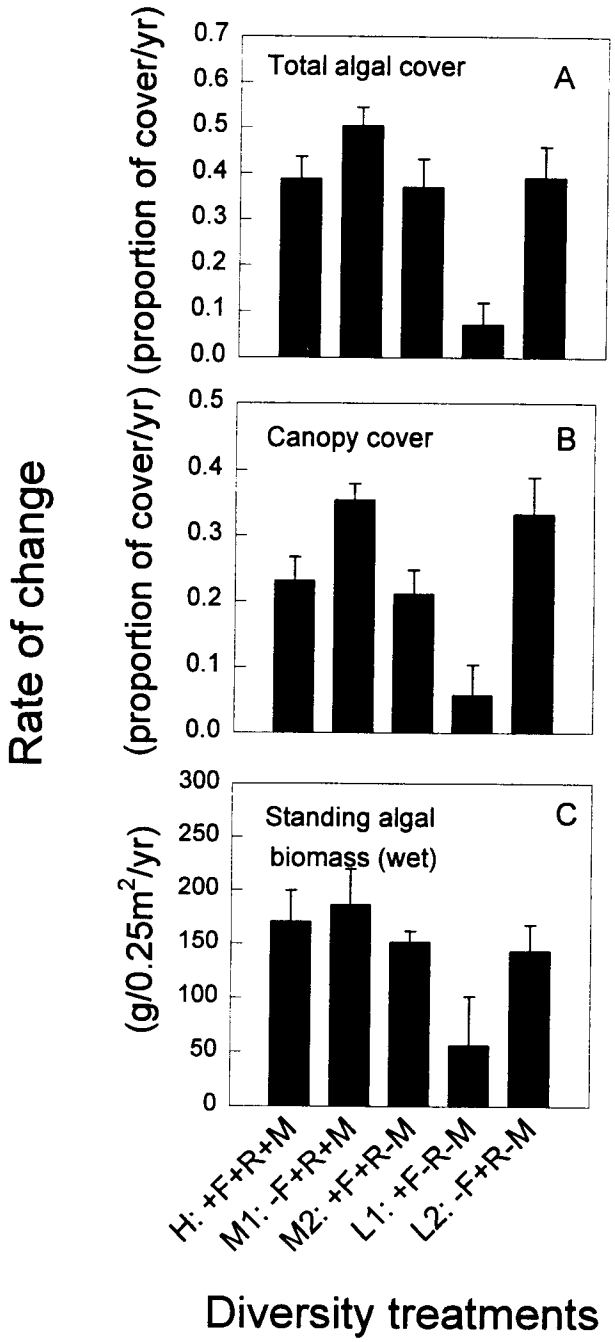

Figure 2.6. Rates of change during diversity press: community measures. See Table 2.4 for analysis. See Figure 2.3 for explanation.

Treatment differences at the completion of the diversity press

At the end of the 15 months of the diversity press phase of the experiment, the treatments differed substantially. Species richness and diversity, as measured by Simpson's index (large values of this index mean low diversity) demonstrate that the experimental regime was effective in creating treatments differing substantially in both the number of species and the relative dominance of the algal species within those treatments (Figure 2.7). The effects of the diversity manipulation on the community measures of algae at the end of the diversity press showed two patterns (Figure 2.8): first, canopy and total algal cover were substantially lower in the low diversity treatments (L1 and L2) and second, standing biomass was lowest in the fucoid-exclusion treatment (M1 and L2).

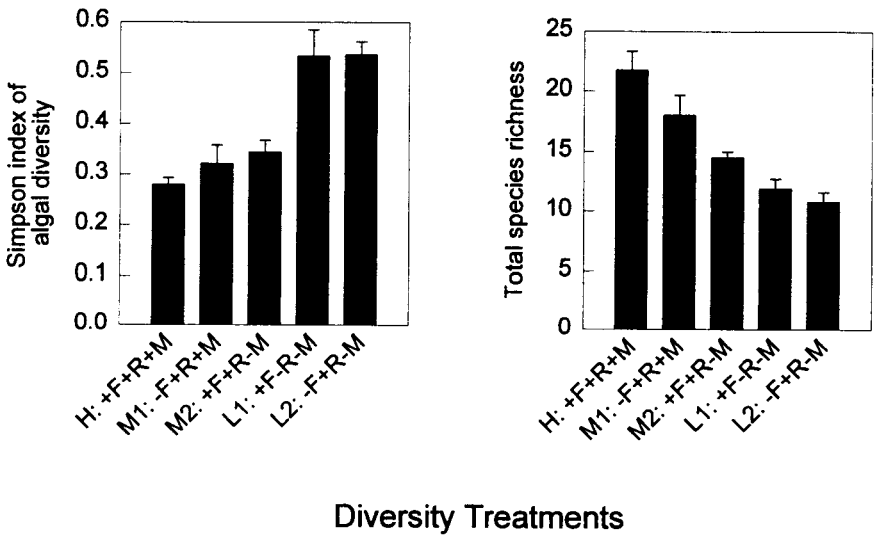

Figure 2.7. Diversity measures at the beginning of the recolonization phase (August 1994). A) Total species richness (all macroscopic floral and faunal species except highly mobile species) for this date. B) Algal dominance as measured by Simpson's index for all algal species. Larger values of the index indicate dominance by individual species. Error bars are standard errors. Ten plots used per treatment.

Figure 2.8. Community measures for all plots at the start of the recolonization phase. A) Total algal cover, B) canopy cover and C) standing algal biomass (wet) by treatment in August 1994. Treatments are arranged by descending diversity. Data for box plots are 8 subsamples (625 cm^2) from every plot; 10 plots in each treatment. The upper and lower edges of each box indicate the 25th and 75th percentile; the solid line within the box is the median and the dotted line is the mean. Open circles outside the whiskers are subsample points beyond the 10th and 90th percentiles.

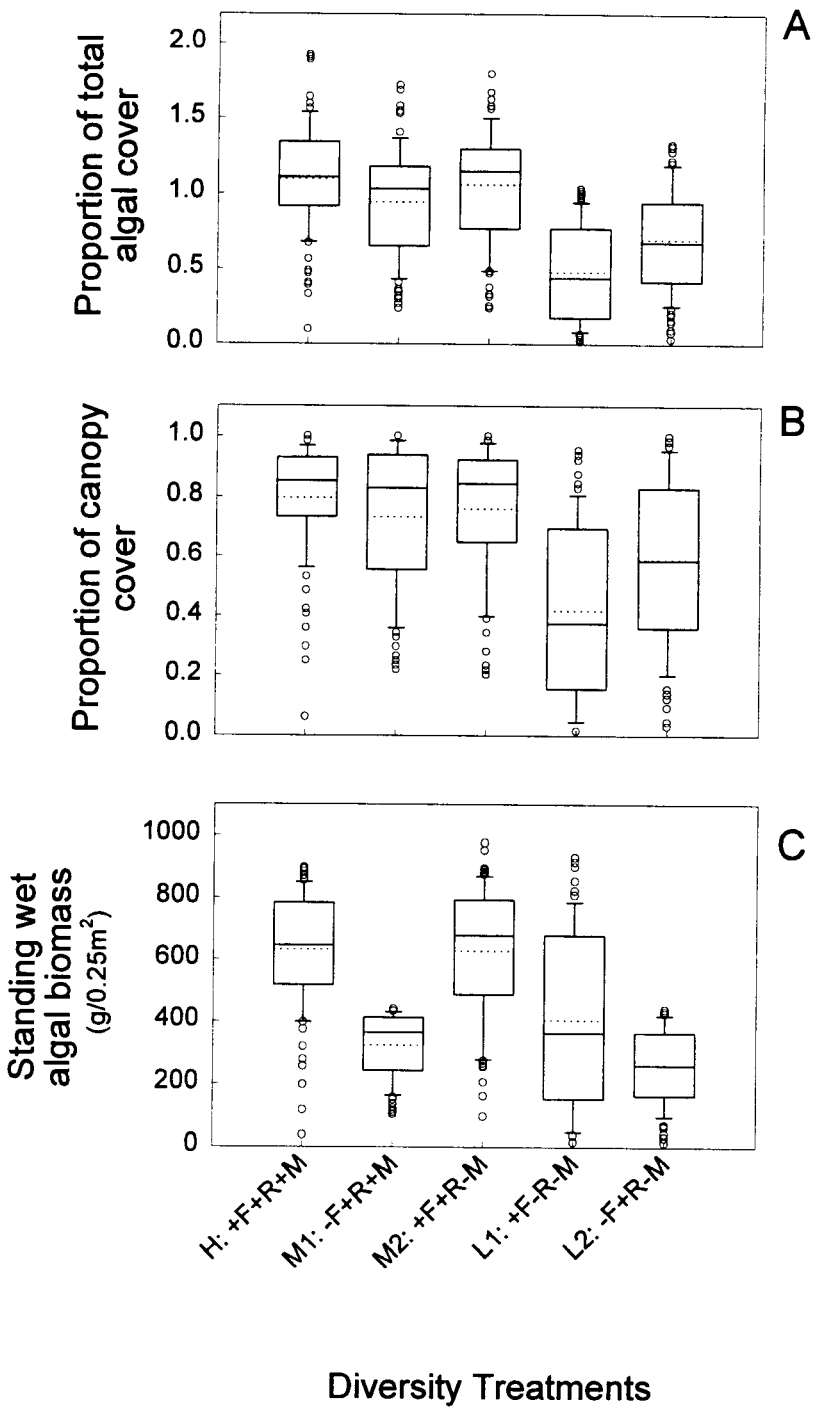
A
Proportion of total algal cover
2.0
1.5
1.0
0.5
0.0
B
Proportion of canopy cover
1.0
0.8
0.6
0.4
0.2
0.0
C
Standing wet algal biomass (g/0.25m²)
1000
800
600
400
200
0
H: +F+R+M
M1: -F+R+M
M2: +F+R-M
L1: +F-R-M
L2: -F+R-M
Diversity Treatments

Figure 2.8

There was only one strong effect on species associated with the algal community (Figure 2.9). Density of whelks (Nucella spp.) was much greater at high diversity than in any diversity reduction treatment. As mentioned earlier, even the density in high diversity plots was low compared to lower zones in the intertidal, where "low" densities are 3x the densities I recorded (Berlow 1995). However, this difference among treatments implies that any Nucella effect that occurs in this zone is dependent on high diversity. Neither limpets nor barnacles differed in abundance with reduced diversity. It should be noted, however, that these data may not fully represent differences for limpets because limpet censuses were performed only during non-desiccating conditions. During desiccating conditions, limpets were commonly found in higher densities under thick fucoid canopies where it was moister and cooler than outside the canopies. Often the limpets under the canopy continued to graze while limpets outside the canopy became inactive, presumably to avoid desiccation stress.

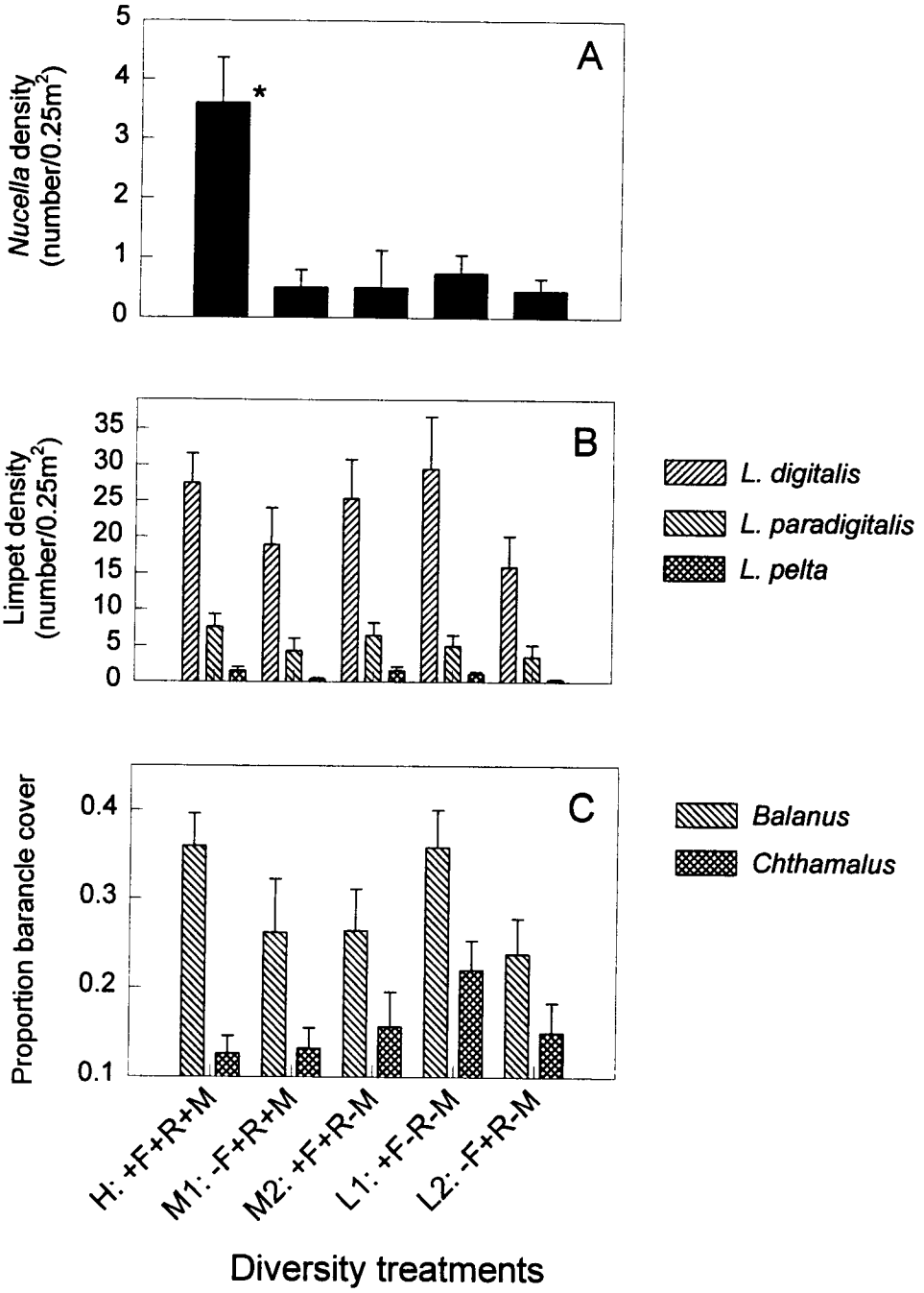

Figure 2.9. Measures of abundance for other species associated with this algal community at the end of the diversity press phase (August 1994). A) Density (#/0.25m^2) of Nucella; B) density of limpets (#/0.25m^2) of the genus Lottia (larger than 0.4 cm); C) barnacle cover. Error bars are standard errors. Ten plots used per treatment. Statistical differences among treatments (p-values): * < 0.05 from a multiple range test. In a MANOVA analysis, there were no significant treatment differences for limpets (TRT: p=0.2838; BLK: p=0.0420) or barnacles (TRT: p=0.1027; BLK: p=0.0002).

Recolonization dynamics

The influence of treatment differences at the start of the recolonization phase were evident in the recolonization dynamics of Pelvetiopsis and, to a lesser extent, of Fucus. Recolonization rates of Pelvetiopsis varied with diversity (Table 2.5B; TIMExTRT interaction). The lowest rates of increase occurred in the lowest diversity treatment (Figure 2.10). Although both Fucus and Cladophora recolonization rates also tended to be higher at higher diversity (Figure 2.10), the differences were not significant (Table 2.5A,D). In contrast, Endocladia recolonization rates tended to be highest in a low diversity treatment, the foliose-reds only treatment (L2), but these differences were also not statistically significant (Table 2.5C).

These variable recolonization rates for Pelvetiopsis appear to be best explained by total algal cover and the degree of dominance at the start of the recolonization phase. As mentioned above, this intertidal zone is particularly susceptible to a strong potential desiccation stress and, because algal cover can ameliorate some of that stress, it might be expected that for species whose recruits are desiccation-sensitive, areas of low algal cover would lead to lower recruitment in general. Areas of very low algal cover at the start of the recolonization period in the lower diversity treatments corresponded to areas of low recovery (Figure 2.11) for Pelvetiopsis. However, this low algal cover is still not enough to explain the strong treatment differences for Pelvetiopsis because even in areas of high canopy cover in the low diversity treatment, Pelvetiopsis recovered more slowly.

Table 2.5. Results of repeated-measure ANOVA for the recolonization dynamics of four species. Dates included in TIME source-of-variation were August 1994 (the last census date during the diversity press for which all species examined were removed) and subsequent censuses: September 1994, March 1995, June 1995, September 1995, January 1996, and May 1996. The census performed in November 1994 had several missing values due to severe weather conditions and was therefore excluded from the analysis. Treatments examined were only those in which the analyzed species was excluded during the diversity press. Five plots per treatment were used. See Table 2.3 for further explanation of labels.

Table 2.5

A. Fucus spp.

BETWEEN SUBJECTS

SOURCE	df	MS	F	P
TRT	1	0.015	0.40	0.5607
BLK	4	0.020	0.53	0.7222
Error	4	0.038		

WITHIN SUBJECTS

		Univariate analysis			Multivariate analysis			
SOURCE	df	MS	F	P	num df	den df	Wilks' λ	P
TIME	4	0.090	14.8	**0.0002**	4	1	0.0080	0.1342
TIME x TRT	4	0.004	0.74	0.5526	4	1	0.0277	0.2475
TIME x BLK	16	0.004	0.71	0.7255	16	3.69	0.0009	0.2704
Error (TIME)	16	0.006						

B. Pelvetiopsis limitata

BETWEEN SUBJECTS

SOURCE	df	MS	F	P
TRT	1	0.086	4.32	0.1062
BLK	4	9.3E-3	0.47	0.7591
Error	4	0.019		

WITHIN SUBJECTS

		Univariate analysis			Multivariate analysis			
SOURCE	df	MS	F	P	num df	den df	Wilks' λ	P
TIME	4	0.065	24.2	**0.0001**	4	1	0.0041	0.0964
TIME x TRT	4	0.012	4.46	**0.0186**	4	1	0.0011	**0.0489**
TIME x BLK	16	0.002	0.58	0.8389	16	3.69	0.0001	0.0787
Error (TIME)	16	0.043						

Table 2.5 continued

C. Endocladia muricata

BETWEEN SUBJECTS

SOURCE	df	MS	F	P
TRT	2	0.014	1.96	0.2028
BLK	4	0.017	2.35	0.1412
Error	8	7.3E-3		

WITHIN SUBJECTS

		Univariate analysis			Multivariate analysis			
SOURCE	df	MS	F	P	num df	den df	Wilks' λ	P
TIME	4	0.063	47.7	**0.0001**	4	5	0.0778	**0.0056**
TIME x TRT	8	0.003	1.94	0.1164	8	10	0.207	0.2700
TIME x BLK	16	0.003	1.96	0.0786	16	15.9	0.0762	0.2953
Error (TIME)	32	0.001						

D. Cladophora columbiana

BETWEEN SUBJECTS

SOURCE	df	MS	F	P
TRT	2	4.4E-3	1.02	0.4044
BLK	4	6.1E-3	1.41	0.3138
Error	8	4.3E-3		

WITHIN SUBJECTS

		Univariate analysis			Multivariate analysis			
SOURCE	df	MS	F	P	num df	den df	Wilks' λ	P
TIME	4	0.007	11.0	**0.0001**	4	5	0.320	0.1563
TIME x TRT	8	7.7E-3	1.30	0.2928	8	10	0.331	0.5357
TIME x BLK	16	5.3E-3	0.90	0.5625	16	15.9	0.148	0.6125
Error (TIME)	32	5.9E-3						

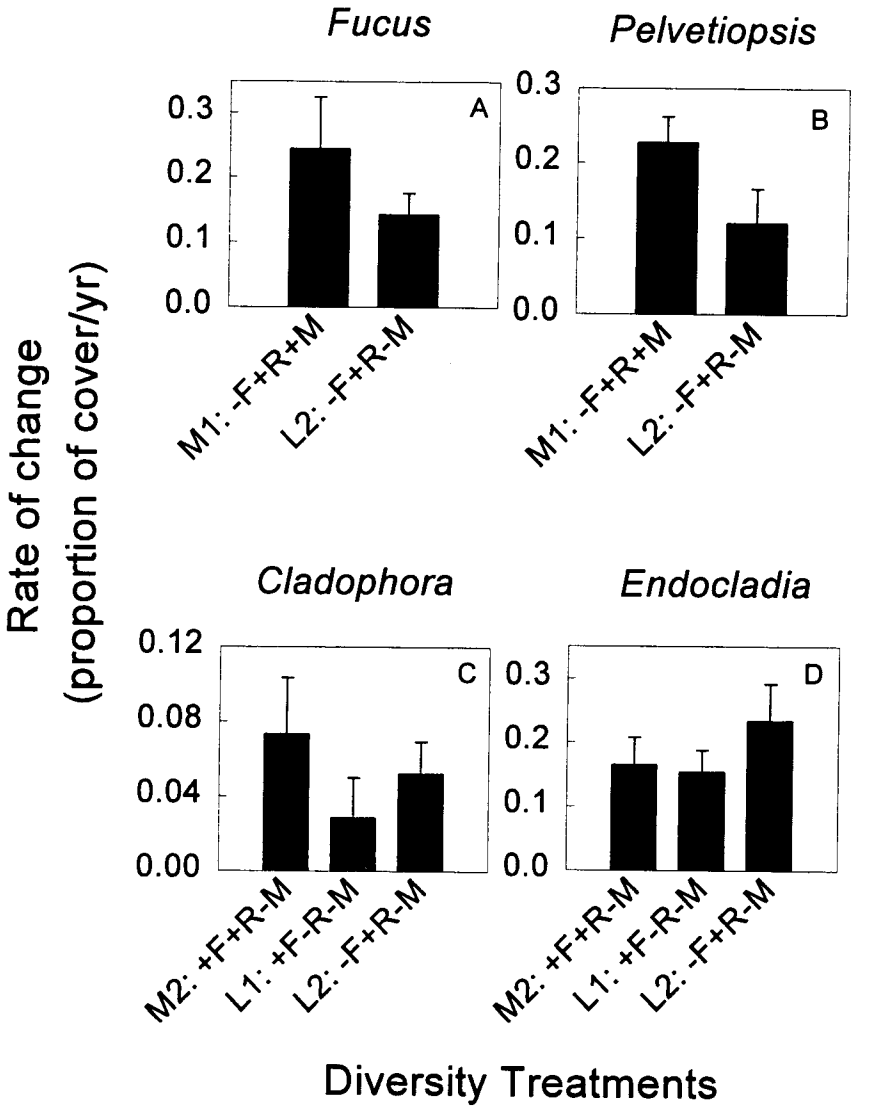

Figure 2.10. Recolonization rates for all species examined. Rates calculated as the slope of the regression of abundance over time during which abundance was still increasing. See Table 2.5 for repeated measures analysis of same data. Error bars are standard errors. Five plots per treatment. Treatments are arranged by descending diversity.

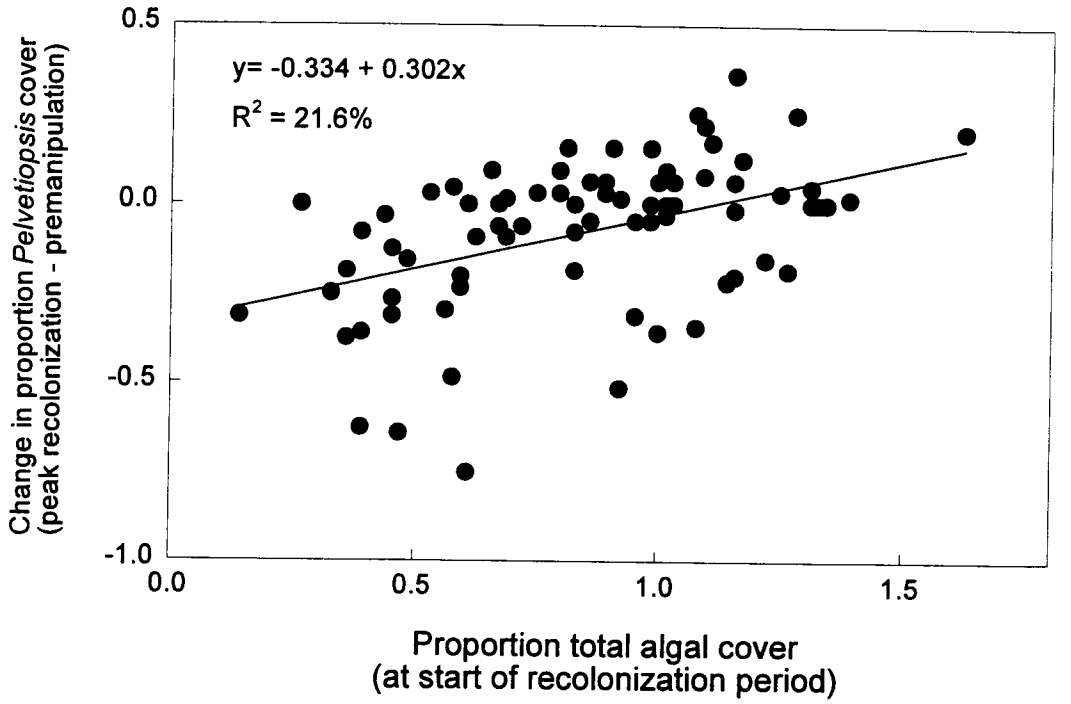

Figure 2.11. Change in Pelvetiopsis cover as a function of total algal cover at the start of the recolonization phase (August 1994) for treatments in which the species had been excluded (M1, L2). Change in cover is the difference between pre-experiment abundance and the peak cover during the recolonization period for all subsamples (8 x 625 cm^2/plot).

Another factor that appears to have influenced the Pelvetiopsis treatment differences was the recolonization in areas of high Mastocarpus cover. In both treatments from which fucoids were excluded, Mastocarpus cover increased much more than treatments including fucoids (Figure 2.4). However, that high cover persisted longer in the foliose red-only treatment (L2). (See Chapter 3 for more details.) As expected, with the increase of Mastocarpus cover, the average patch size of Mastocarpus increased (Figure 2.5). Because Mastocarpus often forms a thick canopy and a high primary cover when it forms such large patches (G. Allison, personal observation), it may effectively reduce recruitment of other species.

If Pelvetiopsis recolonization is examined in just these areas having 100% cover of Mastocarpus at the start of the recolonization phase, Pelvetiopsis rates were much greater in the higher diversity treatments (Figure 2.12). The only difference between the patches in the two treatments is the presence of many more species (the low abundance group) in the higher diversity treatment (M1). Although I cannot distinguish whether Pelvetiopsis recruitment was directly facilitated by the low abundance species group, or that group somehow reduced the competitive dominance or priority effects of Mastocarpus, the sign of the interaction of the low abundance species group on Pelvetiopsis recolonization is positive.

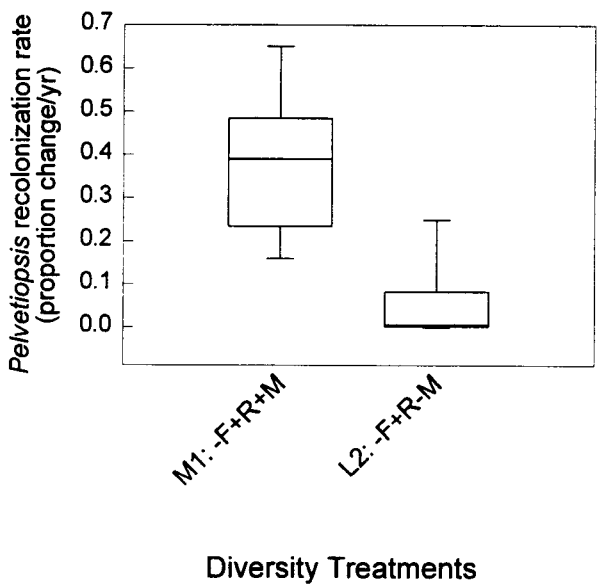

Figure 2.12. Pelvetiopsis recolonization rate within Mastocarpus patches of size > 50 grid points (approximately 500cm^2); n=5 for each treatment. Recolonization rate is change in fraction cover/year. See Figure 2.8 for an explanation of box plot specifics.

Fucus recolonization rates demonstrated patterns similar to those of Pelvetiopsis. First, Fucus recolonization was clearly related to the algal cover of a plot at the start of the recolonization phase (Figure 2.13): low algal cover apparently reduced recolonization rates. Like Pelvetiopsis rates, there was still a large amount of variation unexplained by cover in plots with high cover. However, in sub-subplots with high algal cover (Figure 2.14), recolonization rates were lower in those areas dominated by a few species (i. e., large Simpson index).

Thus, Pelvetiopsis recolonization rates were higher in the high diversity treatment. This pattern seems best explained by the higher algal cover of the higher diversity treatment and the presence of the low abundance species group that somehow facilitated recruitment into Mastocarpus patches. Although the dynamics for other species were not statistically different among treatments, regression analysis suggested that Fucus had a similar pattern.

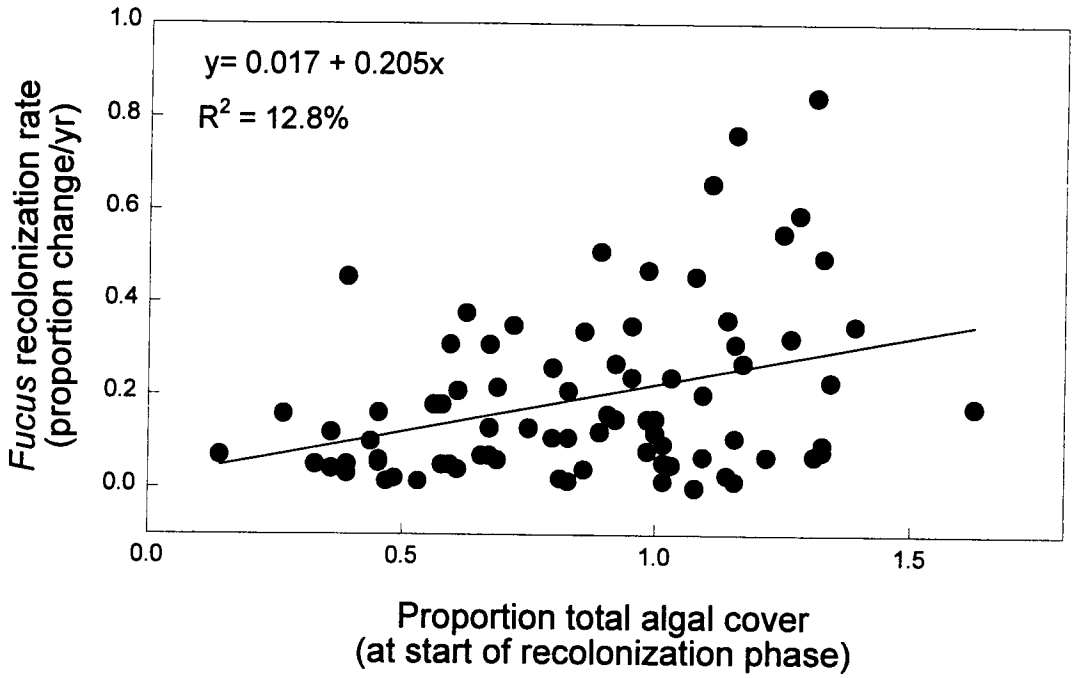

Figure 2.13. Change in Fucus cover as a function of algal cover at the start of the recolonization phase (August 1994). Illustrated are the rates of change of Fucus in each 625 cm^2 subsample from all plots in both recolonization treatments (M1 and L2).

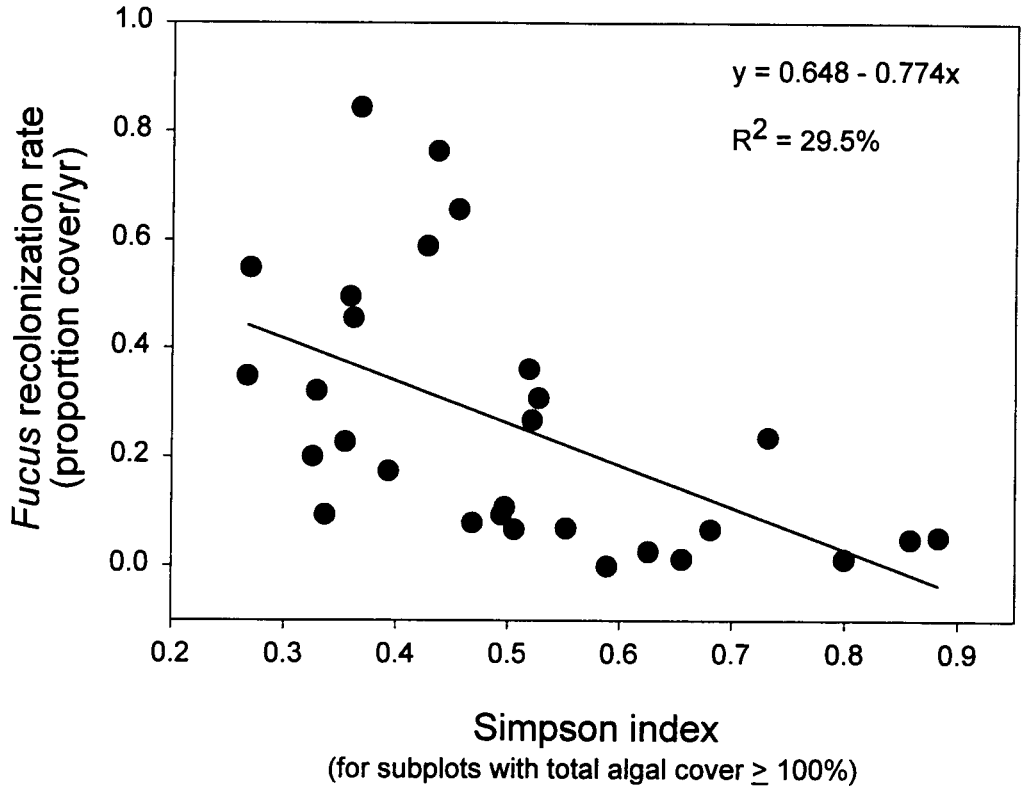

Figure 2.14. Fucus recolonization as a function of dominance of resident species. Illustrated are the rates of change of Fucus in all 625 cm^2 subsamples in both recolonization treatments (M1 and L2) that had an total algal cover ≥ 100%. The Simpson index was calculated from the abundance of all algal species in the subplot at the start of the recolonization phase and is a measure of the dominance of few species.

The interaction of physical stress and diversity

Because the plots of the experiment covered so much area in the high zone at this site (greater that 50 m^2), they covered a sizable desiccation gradient. The desiccation potential was measured by two physical correlates of desiccation stress, emersion time and north/south substratum angle. To examine the influence of this gradient on community dynamics, I used regression analysis of the physical correlates on rates of change in both the diversity press and recolonization phases of the experiment.

There were significant correlations between the dynamics in only some treatments and measures of desiccation potential (Figure 2.15) that suggest a strong effect of diversity reduction. In all cases, the treatments with a significant correlation between rate of change and desiccation potential were low diversity treatments. Higher diversity treatments showed little difference in rate across the gradient indicating that these treatments buffered the effects of the stress.

Figure 2.15. Influence of the desiccation gradient on community dynamics among treatments. Regression of measures of desiccation potential (relative emersion index and substratum angle) against the rates of change during the diversity press (A=Fucus, B=Pelvetiopsis, C=Mazzaella, D= standing algal biomass (wet)) and the recolonization phase (E = Fucus). Only those regression are shown in which there were treatment differences in the slope of at least one of the desiccation variables. Desiccation potential ranges from low (0) to high (1) relative to the range within all plots of the experiment. '*' = regressions that are significant at the $\alpha = 0.05$ level.

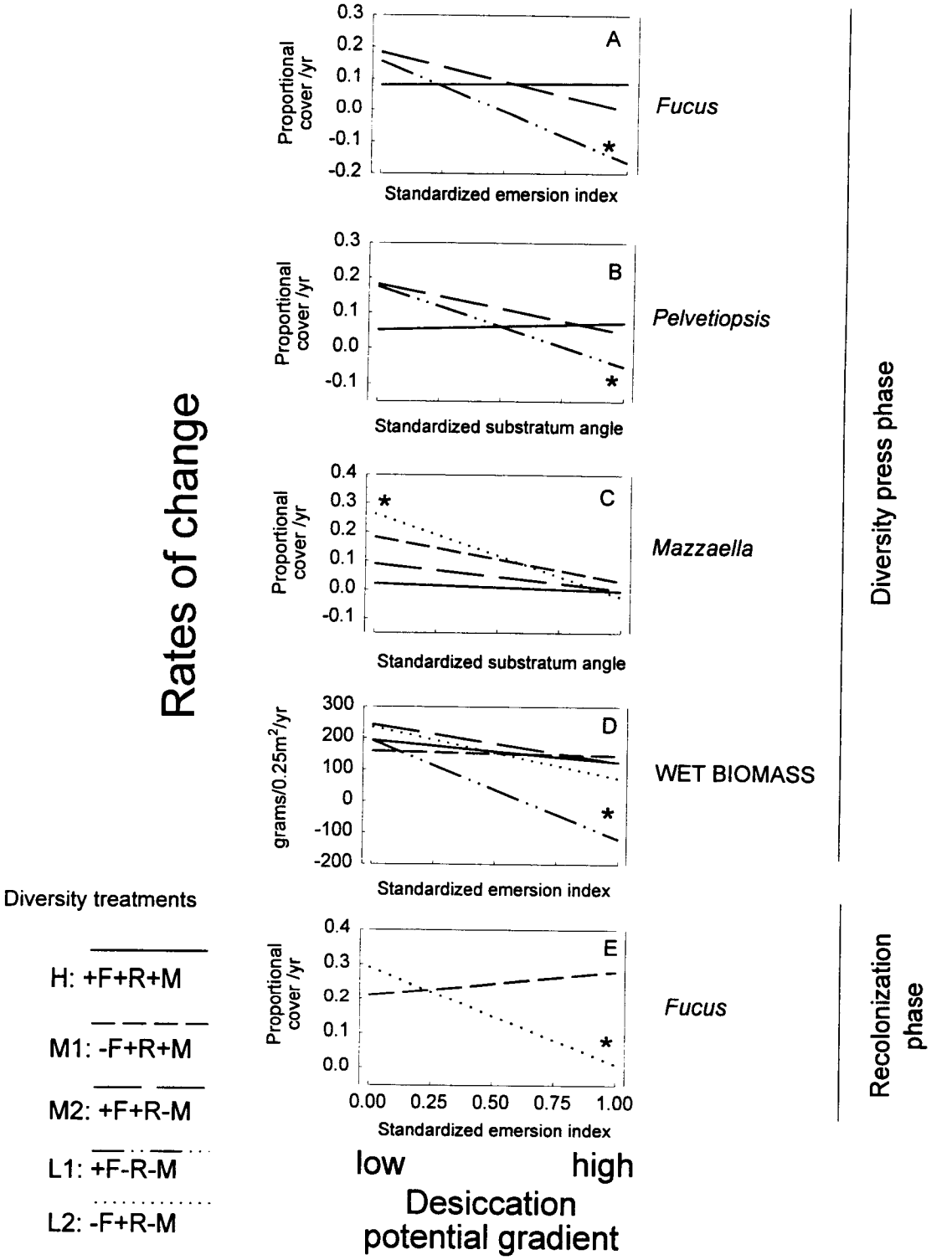
Rates of change
Proportional cover /yr
A
Fucus
Standardized emersion index
B
Pelvetiopsis
Standardized substratum angle
C
Mazzaella
Standardized substratum angle
grams/0.25m²/yr
D
WET BIOMASS
Standardized emersion index
Diversity press phase
Diversity treatments
H: +F+R+M
M1: -F+R+M
M2: +F+R-M
L1: +F-R-M
L2: -F+R-M
E
Fucus
Recolonization phase
low
high
Desiccation potential gradient

Figure 2.15

Furthermore, how these low diversity treatments differed from the high diversity treatment indicate how the interactions with other species groups change across the gradient. In the low diversity treatment (L1: +F-R-M) in Figure 2.15A,B, at the high stress end of the gradient, the rates for both Fucus and Pelvetiopsis are lower than in the high diversity treatment. This suggests a positive interaction with Fucus and Pelvetiopsis of the species that were removed (foliose reds). However, at the low stress end of the gradient, both species were negatively affected in the higher diversity treatments, that is, removal of other species increased the abundance of Fucus and Pelvetiopsis. Thus, the sign of the interactions on those species changed across this gradient. This pattern is similar for Fucus in the recolonization phase (Figure 2.15E) when comparing the higher diversity treatment (M1) to the lower diversity treatment (L2). For Mazzaella in the highest stress, there is little difference among treatments (Figure 2.15C) but at lower stress, the rates in the lower diversity treatment (foliose-reds only; L2) are much greater than the high diversity treatments. This implies a strong competitive effect of the fucoids (compare H, M2 to M1, L2) in low stress, but little interaction with the fucoids at high stress. Finally, the rates of change in wet biomass were only different at the high stress end of the gradient for the low diversity (L1: +F-R-M) treatment (Figure 2.15D). This indicates that the species in this treatment compensated for reduction of diversity on total algal biomass at lower stress but not at high stress.

Diversity Regressions

In general, algal species richness was a poor predictor of the variation in dynamics during the press phase. In a linear regression analysis (Table 2.6; Figure 2.16), species number was a significant predictor for the variation in the rates of change for only Mastocarpus and total algal cover. Even then, richness explained only a small amount of the variation (R^2: Mastocarpus=4.8%, total algal cover=9.5%).

DISCUSSION

Reduction of diversity clearly had important effects at both the species and community levels and these effects were caused by the loss of both strong negative and strong positive interactions. Canopy cover, although dominated by fucoids in high diversity treatments, was compensated by the increases in Mastocarpus and Mazzaella in the absence of fucoids. This strong competitive release was one of the most pronounced effects of the diversity manipulation and attributable primarily to the negative effect of fucoids on the foliose reds. However, another strong effect evident in all community measures was low fucoid cover in treatments from which all other algal species were removed. Another apparent positive interaction was the effect of the low abundance species group on Pelvetiopsis recolonization; reduced diversity treatments experienced slower recolonization rates at least partially attributable to the absence of the low abundance species.

Table 2.6. Regression of species and community dynamics with total algal richness. Results of linear regression of total algal species richness with the rates of change during A) diversity press phase and B) recolonization phase. Parameters reported are intercept estimates (and p-value) and the slope of the relationship (and p-value). P-values in bold are significant at the $\alpha = 0.05$ level.

A. Diversity Press Phase:

Rate of change in:	Intercept parameter	Intercept p-value	Species richness slope parameter	Species richness (p-value)
Fucus	0.00486	0.3186	0.000141	0.9079
Pelvetiopsis	0.00369	0.2880	0.000680	0.4360
Mastocarpus	0.0286	**0.0001**	-0.00333	**0.0084**
Mazzaella	0.00627	0.0943	-0.000284	0.7443
Total algal cover	0.0135	**0.0178**	0.00436	**0.0037**
Canopy cover	0.0152	**0.0014**	0.00131	0.2629
Standing algal biomass (wet)	8.81	**0.0031**	0.857	0.2496

B. Recolonization Phase:

Rate of change in:	Intercept parameter	Intercept p-value	Species richness slope parameter	Species richness (p-value)
Fucus	0.00371	0.6127	0.00361	0.0822
Pelvetiopsis	0.00921	0.1515	0.00152	0.3389
Endocladia	0.01649	0.0187	-0.00047	0.8434
Cladophora	0.00124	0.7049	0.00124	0.3301

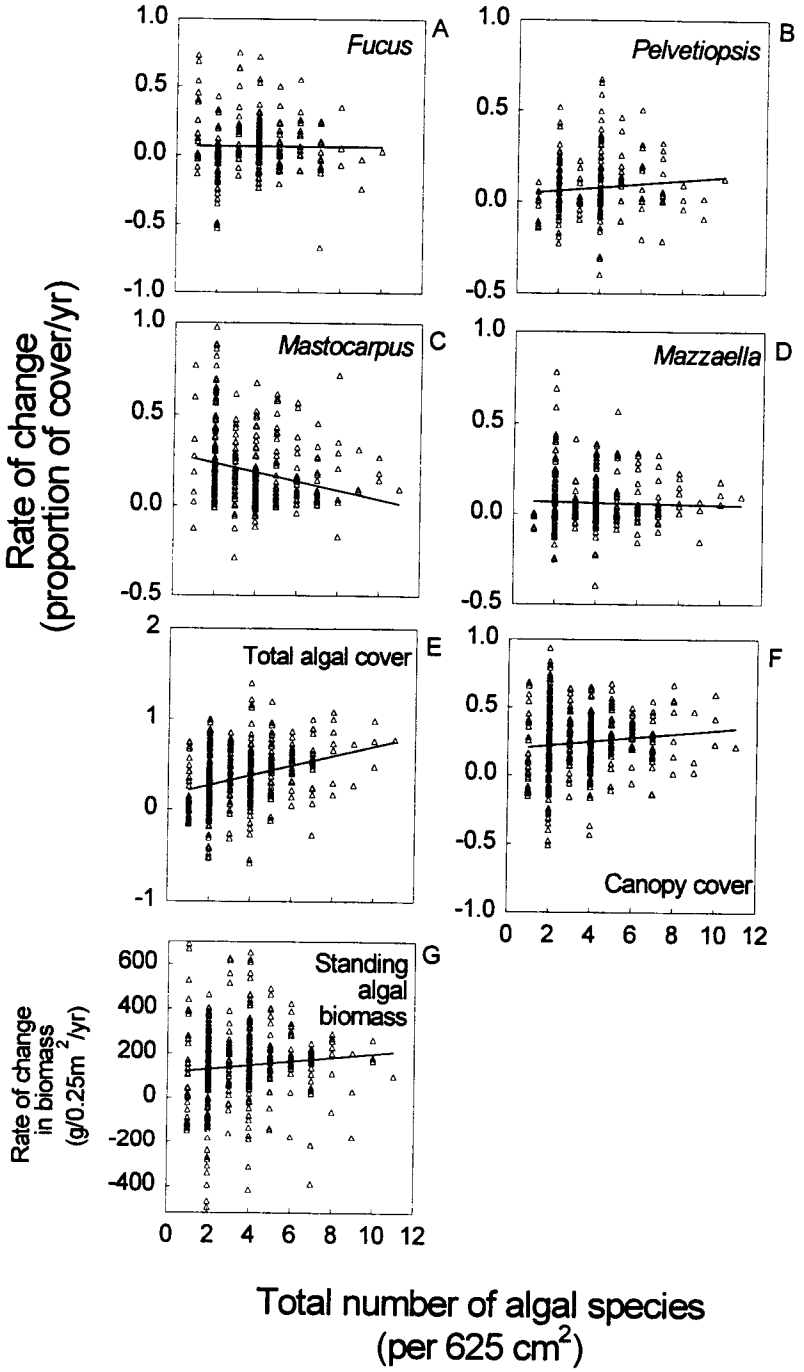

Figure 2.16. Regression of species and community dynamics during the diversity press with total algal richness. Species measures are shown in A-D, community measures in E-G. Each datum is a 625 cm^2 sub-subplot.

For some species, the magnitude of treatment effects was small, even though the treatments represented a large range of diversity. During the diversity press phase of the experiment there were no significant TRT or TIMExTRT effects for the fucoids (or for Endocladia or Cladophora (data not presented)). Further, the recolonization dynamics of Endocladia and Cladophora were not strongly affected by the treatment regime. For these measures lacking treatment effects, any effects of other species were either non-existent or overwhelmed by external factors. Thus, within the experiment there were examples of strong positive, strong negative and weak interactions.

Positive interactions were common and increased in importance with increasing stress. As mentioned earlier, it has been suggested that harsh physical environments may be conducive to positive interactions (Bertness and Callaway 1993, Bertness and Hacker 1994, Callaway and Walker in press) and that as physical stress increases, interactions may become qualitatively more positive. Although the strongest effect (fucoids on Mastocarpus) was clearly a negative interaction, there were suggestions of many positive interactions. The low rates of change during the diversity press for Fucus (and somewhat for Pelvetiopsis) in the low diversity treatment suggest a positive interaction with the other species present in the high diversity treatments. The higher rate of recolonization for Pelvetiopsis in the higher diversity treatment suggest that the low abundance species either directly facilitated recruitment or somehow prevented monopolization by Mastocarpus.

However, the strongest indication that positive interactions increase with physical stress is how treatment effects interacted with the desiccation factors (Figure 2.15). In all of those measures, loss of species increased the influence of the desiccation gradient

suggesting that higher diversity ameliorated some of the effects of the stress gradient. Indeed, it only became evident that there was a significant desiccation gradient across the experiment after the diversity manipulation was performed. Furthermore, even for Mazzaella, for which the interactions with the other algal groups were apparently never positive, the strength of the negative interactions decreased with increasing stress. A qualitative interaction web summarizes the interactions from low to high stress (Figure 2.17) during the press phase.

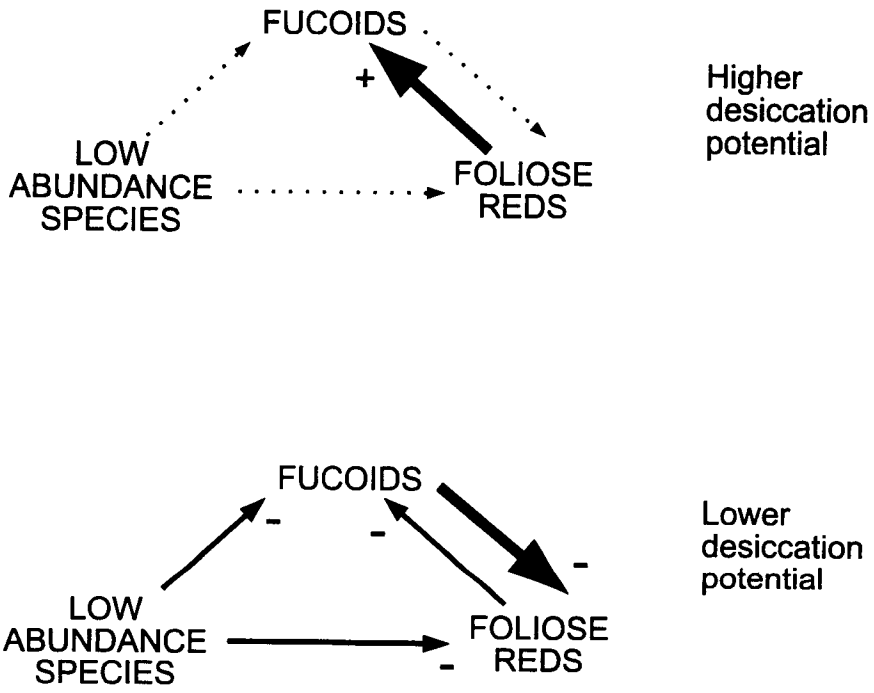

Figure 2.17. Interaction web summarizing differences between higher and lower stress areas for the diversity press phase of the experiment. Line thickness indicates strength of interaction and '+' or '–' indicates the sign of the interaction. Dotted lines indicate apparently weak effects. Interactions not indicated with arrows could not be evaluated with this experimental design. Interactions uncovered during the recolonization period (i. e., the positive effect of low abundance species on Pelvetiopsis recolonization) are not shown.

Even though there were several effects caused by the diversity treatments, species number was a poor predictor of the changes in this experiment because effects were highly dependent on which species were involved in the interaction. This is not to suggest that low abundance species had no effect; their effect on Pelvetiopsis recolonization was clear. Rather, species number did not represent the character of the community that had the most effect. For instance, +fucoid and –fucoid treatments differed by only two species but produced important effects on the foliose red species. On the other hand, the difference between the high diversity treatment (H) and the –low-abundance treatment (M2) differed by many species but did not differ substantially in most other measures.

Identifying factors that influence diversity effects

As I have suggested, one important motivation within biodiversity research is to understand how diversity loss will impact communities and ecosystems. But if species number is a poor predictor of such changes, as these data and other studies (Schulze and Mooney 1993b, Denslow 1996, Ewel and Bigelow 1996, Huston and Gilbert 1996) suggest, how might we get closer to the goal of predicting where the effects of diversity loss will be the most severe? At least two approaches appear promising in this regard. The first is quantifying the interactions among species in susceptible communities through experimental investigation. This is the most direct approach, and in situations in which it has been used, has provided invaluable information. By accumulating detailed information from different systems with this approach, we may determine the types of systems that may be most susceptible to severe changes from diversity loss. However,

this approach is also time consuming, expensive, and may not be logistically feasible for many community types.

The second approach, outlined in the introduction, is a comparative/experimental approach that uses known characteristics of communities to identify communities more likely to experience strong effects from the loss of species. The approach is indirect in that it infers how environmental conditions (and other factors) influence the species interactions of a community and therefore the potential effects of loss of diversity. While this may serve only as a rough guide, the results from this experiment suggest that it may be a useful approach: the effects of the reduction of diversity were greatest where physical stress was the harshest, which would have been expected from predictions of effects on interaction strengths. The success and power of this approach will depend upon the degree to which factors that influence species interactions within communities can be identified. Below I summarize some of the factors that are expected to influence the strength, sign and distribution of species interactions.

Factors that should influence interaction strength include abiotic stress, recruitment and habitat heterogeneity. Physical conditions may weaken interactions if they induce physiological stress that inhibits interaction capabilities or directly interferes with an interaction. Examples of such stresses in the intertidal include desiccation stress (Menge 1978a, b, Lowell 1984, Bell 1993, Davison et al. 1993, Chapman 1995, Davison and Pearson 1996), sand inundation (Menge et al. 1994), and wave stress (Menge 1978b, Denny 1995); see Menge and Sutherland (1987) and Menge and Farrell (1989) for reviews. While these factors may modify interactions in a predictable way, it should be

noted that community outcome of an abiotic stress will often depend on which species in an interaction is more affected by the stress (Menge and Olson 1990).

Recruitment limitation can weaken otherwise strong interactions by simply reducing the number of interacting organisms (Gaines and Roughgarden 1985, Menge and Sutherland 1987). Comparisons of situations where recruitment is high and low have often shown density-dependent effects at high levels but that at low levels, adult population sizes are strongly influenced by the recruitment level (Gaines and Roughgarden 1985, Forrester 1990, Jones 1990, 1991, Hixon 1991, Menge 1991, Caley et al. 1996).

High heterogeneity within a habitat can lead to extensive coexistence among species that would otherwise be excluded or severely reduced. Such heterogeneity can reduce the overall competition or predation among species by providing more diverse habitat or refuges from strong negative interactions (Menge 1976, Menge and Lubchenco 1981, Lubchenco 1983, Menge et al. 1985, Hixon and Menge 1991, Hixon and Beets 1993, Carr 1994, Berlow and Navarrete 1996). Still other factors may influence interaction strength such as productivity (Menge et al. 1996)

The second aspect of species interaction that will affect the influence of diversity is the sign of interactions. As mentioned earlier, recent research has suggested some broad patterns of the prevalence of positive interactions. For example, it has been demonstrated that positive interactions are more common in areas of high physical stress where "neighbor" effects ameliorate stress, but are less common in physically more benign areas where competition becomes more important (Bertness and Callaway 1993, Callaway 1995, Bertness and Leonard in press). Thus strong abiotic factors may actually

change the sign of interactions (Bertness 1989, Bertness and Hacker 1994, Bertness and Yeh 1994; Figure 2.15A,B) or these factors may weaken interaction (Figure 2.15C, 2.17). In both cases however, the implications for loss of diversity are similar: the reduction of the system's ability to compensate for the loss.

The third aspect of interactions that will influence how well we will be able to predict the consequences of a diversity change is the distribution of interaction strengths within a community. In some case, species within a functional group, such as a guild, may be (approximately) functionally equivalent. In such a case, remaining species of the group may completely compensate for the loss of some species— that is, there has been a change within a group, but the community properties remain as before (Chapin et al. 1995). However, numerous experiments have demonstrated that some communities can be profoundly influenced by a single species, whereas other species have no discernible impact on the community (for reviews see Menge et al. 1994, Power et al. 1996). In such cases, the distribution of interaction strengths is strongly skewed and to understand how loss of a species will affect the community requires that the characteristics of the species are known. Factors that may skew the distribution of interaction strength include: relative abundance (highly abundant species are likely to have important roles) and the presence of species with unique characteristics such as species that fix nitrogen, species that modify the disturbance regime of a community, or species that perform a keystone consumer role (Chapin et al. 1995). While the characteristics of keystones are still difficult to distinguish a priori (Menge et al. 1994), with a modest amount of natural history investigation and short-term experimentation, approximate community dynamics can be predicted.

One prediction that could be made from these results and models is that among communities that have the roughly the same species composition, the strongest consequences of loss of diversity will occur under the most physically stressful conditions. Thus organisms at the edge of their species' geographic range, or in potentially high stress or degraded habitats may be most vulnerable to the effects of species loss in their community. Further, effects of particularly stressful periods, such as droughts and El Niños, may be more severe if biodiversity is reduced. Clearly there will be places and times where loss of diversity will have important implications and others where it will have little. As has been suggested before, understanding which are the important interactions within a community and how those interactions are modified by human actions will go a long way in helping us understand the consequences of our actions.

CHAPTER 3

Resistance and Resilience to a Pulse Perturbation in a Rocky Intertidal Community: The Influence of Diversity and Stress Intensity on Community Dynamics

ABSTRACT

The role of species diversity in the resistance and resilience of an intertidal community was tested using an experimentally-induced heat stress that was applied at the end of a 15 month long reduction in diversity. This thermal perturbation produced a gradient of thermal stress within plots and, consequently, different levels of disturbance. The magnitude of the effect of the thermal stress was determined largely by the pre-stress values of the analyzed measures (cover of dominant species, total algal cover, and standing biomass). Because higher diversity treatments (especially those with the dominant algal group, fucoids) had, on average, higher overall abundance, these treatments were the most severely affected in absolute loss. The stress was also relatively non-selective in that the dominant algal species were reduced in roughly equivalent proportions, suggesting an important distinction for predicting when diversity may influence community dynamics. However, one form of diversity that was roughly equivalent to structural complexity apparently ameliorated the severity of effects of the perturbation on overall canopy cover. The second component of community dynamics

measured, recovery to a premanipulation reference state, was highly dependent on initial diversity and the degree of disturbance. The reference condition for this community was dominated by persistent fucoid states. States dominated by foliose-red algae also persisted, but were minor in overall community representation. Areas severely disturbed by the thermal stress followed similar recovery patterns regardless of initial diversity, although some differences emerged among diversity treatments by the end of the monitored period. Low diversity plots without fucoids that did not receive the thermal stress in diversity treatments remained in states unlike the reference plots for most of the monitored resilience period. But plots in high diversity treatments, even areas within plots that had experienced moderate disturbance, returned to states similar to the reference quickly. This experiment demonstrated that the effects of the reduction of diversity on community dynamics will be highly dependent on which species are removed as well as on the characteristics of the stress.

INTRODUCTION

Two factors important to the dynamics of an ecological community are the magnitude of change due to some stress (often called "resistance") and how quickly the community recovers from the stress (often called "resilience") (Orians 1975, Pimm 1991, Tilman and Downing 1994). These factors will, to some extent, determine temporal and spatial dynamics of a community by determining the degree of fluctuations from a given perturbation and by determining the proportion of a community recovering at any given

time. These dynamics will, in turn, influence many community properties such as the long-term persistence of communities (Pimm 1991, Grimm et al. 1992) and the regulation of different community structures (Levin and Paine 1974, DeAngelis and Waterhouse 1987, Wu and Loucks 1995).

How these dynamics are influenced by diversity has received extensive theoretical attention. Early work focused on whether highly diverse communities were intrinsically more stable than low diversity communities (May 1971, 1972, Harrison 1979, Pimm 1979, Nunney 1980, Armstrong 1982). Much of this work undermined a common assumption of the time that diverse systems were more stable (e. g., MacArthur 1955, Elton 1958, Hutchinson 1959). These newer analytical models often indicated that complex systems were *not* mathematically more stable than simple systems and often were more fragile.

Much of the historical interest in this topic was based on a comparison of high diversity communities in one place with low diversity communities elsewhere. The motivation for these comparisons was to determine larger patterns of diversity and how, for example, tropical systems differed from temperate systems (Hutchinson 1959, Watt 1964, Wolda 1978). Because of increasing concern about the loss of diversity in many systems (Lubchenco et al. 1991, United Nations Environment Programme 1995), recent interest in this topic has expanded to include how loss of diversity within a given system may influence other ecological properties (Solbrig 1991, Schulze and Mooney 1993a, Mooney et al. 1996). As such, the topic of the effect of diversity on resistance and resilience has application to management issues. Human uses of natural systems often decrease diversity by directly removing component species through activities such as

logging and fishing, by intentionally maintaining low diversity systems (e. g., agriculture), or indirectly through fragmenting landscapes and polluting. Understanding how such diversity changes influence the underlying dynamics of a community is thus important to our ability to successfully manage populations and ecosystems in a sustainable way (Watt 1968, Holling 1973, Gunderson et al. 1995) .

Experimental studies performed on communities that differed naturally in diversity level have suggested that diverse communities may indeed be more stable in response to disturbances. Studies in old fields suggested that primary productivity of diverse communities was more resistant to a nutrient pulse than less diverse communities (Mellinger and McNaughton 1975), although consumer biomass showed less consistent results (Hurd et al. 1971, McNaughton 1993). Studies in Serengeti grazing ecosystems (McNaughton 1977, 1985) demonstrated that higher diversity savannas were more resistant and resilient to change caused by grazing (see McNaughton (1993) for a review). The effects of the 1988 drought in Yellowstone on species composition were apparently modified by the diversity of the communities: diverse areas were more resistant to composition change during the drought (Frank and McNaughton 1991). However, because such studies rely on natural differences in diversity among communities, it is often difficult to separate the effects of diversity from what causes the diversity differences. Doing so is especially critical if we are to understand how *loss* of diversity will change community dynamics. While experimentally manipulating species diversity is perhaps the best solution to these confounding effects, this topic has received little experimental attention (McNaughton 1977, 1988, Johnson et al. 1996, Kareiva 1996).

One recent experiment that manipulated diversity and monitored the resulting community dynamics was a study of grassland species in Cedar Creek, Minnesota (Tilman and Downing 1994, Tilman 1996). In this study, a diversity gradient across sets of experimental plots was established by a gradient of nutrient additions. These experimental plots experienced an extensive natural drought several years after the diversity gradient was established. Although some of the effects observed in the experiment may be attributable to the nutrient manipulation, the results were nonetheless intriguing. First, the proportional amount of biomass lost due to the drought was related to the diversity of the plot: areas dominated by only a few species experienced the greatest loss. Second, biomass recovered to pre-drought levels more quickly in higher diversity plots. Both results suggested a positive role of higher diversity in ameliorating the community level effects of the stress.

Ecological communities are subjected to numerous kinds of disturbances (Sousa 1984b, Pickett and White 1985) both natural (e. g., extreme temperatures, storms, fires, landslides) and human-induced (e. g., oil spills, dredging, clearcuts) and the characteristics of these perturbations should determine their overall community effects. For example, a shrubland fire that burns with intense heat has a very different impact upon the recovery of a shrubland than a quick, less-intense fire (Christensen 1985). The effects of disturbance *on* diversity are influenced by frequency (Huston 1979), phasing (Abugov 1982) and intensity (Malanson 1984) of disturbances. Whether characteristics of disturbance are influenced *by* diversity is rarely addressed.

Benthic marine communities have been productive systems to study community dynamics and the responses to stresses (Sutherland 1974, 1981, Sousa 1979a, b, Paine

and Levin 1981, Farrell 1988). These communities often have a relatively rapid recovery rate from disturbance, have organisms that are relatively easy to manipulate, and are of a convenient scale for experiments (Connell 1974, Paine 1977). Furthermore, natural disturbances are common in many of these communities, and a great deal is already understood about their disturbance and succession dynamics (e. g., Sousa 1979a, b, 1980, Paine and Levin 1981, McGuinness 1987, Farrell 1988, 1989, 1991).

In this chapter, I present the results of an experiment in the high zone of the rocky intertidal in which an artificially created thermal stress, designed to mimic natural phenomena, was applied to experimental plots that differed in diversity. This diversity gradient was created by an experimental manipulation of macroalgal species. I determined the magnitude of the effects of the thermal stress on the different diversity treatments and followed the recovery of the community from the stress.

The questions that I addressed with this experiment are: How does diversity influence the magnitude of the effect of this pulse perturbation? How does the initial deviation from original reference points (reduced diversity treatments are less similar to the reference plots) affect recovery from the thermal stress and the diversity press? How does diversity interact with the disturbance level? In general, the results from this study indicate that species reductions strongly modified the effects of the perturbation, both in the degree to which the community was affected and its recovery from the stress.

SYSTEM DESCRIPTION

I performed this study in the high intertidal zone of the rocky benches of Fogarty Creek Point (44° 51' N, 124° 03' W), on the central coast of Oregon, USA. Several aspects of this site have been described (Farrell 1989, 1991, Blanchette 1994, Berlow 1995, Navarrete 1996) and some details of this experiment are outlined in Chapter 2. The low zone of this site is composed of a mosaic of kelps, seagrass and urchins and the mid zone is dominated by beds of the mussel Mytilus californianus. The high zone is dominated by macroalgae (mostly fucoid species, Fucus gardneri and Pelvetiopsis limitata, and foliose red species, Mastocarpus papillatus and Mazzaella (=Iridaea) cornucopiae), which together comprise approximately 94% cover on average (including overlapping layers) and acorn barnacles (mostly Balanus glandula and Chthamalus dalli). Numerous other macroalgal species also exist in this zone, though usually at low abundance (see Table 2.1). The most common of these low abundance species were Endocladia muricata and Cladophora columbiana, which can occur locally in high abundance. The experiment was performed across an extensive portion of the site, near the main point, in areas where exposure to wave energy ranged from moderately protected to moderately exposed.

Because the high intertidal zone is characterized by less frequent immersion than lower zones, it is subjected to a high desiccation potential. Although the common species of this zone are highly adapted to these conditions (Glynn 1965, Schonbeck and Norton 1979a, b, Lüning 1990, Davison and Pearson 1996), severe heat or desiccation stress can

still cause high mortality (Taylor and Littler 1982, Lüning and Freshwater 1988, Olson 1992, Bell 1993, Chapman 1995).

METHODS

Diversity treatments

The experimental gradient of diversity used in this study was created by removing macroalgal species from initially high diversity plots. First, ten 1 m^2 plots were randomly assigned to each treatment in a randomized block design with two replicates per block. I created different diversity treatments by removing different numbers of three algal groups (1: the fucoids, 2: the foliose reds and 3: all other macroalgal species, termed "low abundance species"). Thus a high diversity treatment had all three groups, a mid diversity treatment had two groups and a low diversity treatment had only one of the three algal groups. Different combinations of these groups formed two different mid diversity treatments and two different low diversity treatments (Table 3.1). A full factorial design was not possible because of limited experimental space at this site. The diversity treatments were initiated in April 1993 and maintained for 15 months (until August 1994) by removing recruits of all excluded species at least every two weeks. This 15 month "diversity press" phase was detailed in Chapter 2. All phases of the experiment are diagrammed in Figure 3.1.

Table 3.1. Experimental treatment structure and the diversity within treatments. All macroalgal species were lumped into one of the three groups: fucoids = Fucus spp. and Pelvetiopsis limitata; foliose reds = Mastocarpus papillatus, Mazzaella (=Iridaea) cornucopiae; low abundance species = all other macroalgal species including Endocladia muricata and Cladophora columbiana (see Table 2.1 for a complete list). '+' = group included in the treatment, '–' = group excluded from the treatment. Average species richness per plot throughout diversity press phase includes all macro-flora and fauna except very small or highly mobile species. SE = standard error of species richness. Throughout this paper, either the full code (e. g., "L1:+F-R-M") or the reduced codes are used to refer to the diversity treatments. In the full codes, "F" refers to fucoid, "R" to foliose reds and "M" to low abundance species group.

		Algal groups manipulated			
Diversity Treatment Code	Diversity Treatment level	Fucoids	Foliose Reds	Low abundance species	Average species richness (SE)
H:+F+R+M	high	+	+	+	27.4 (1.81)
M1:-F+R+M	moderate	–	+	+	24.3 (2.00)
M2:+F+R-M	moderate	+	+	–	18.9 (0.43)
L1:+F-R-M	low	+	–	–	15.0 (1.02)
L2:-F+R-M	low	–	+	–	13.3 (0.75)

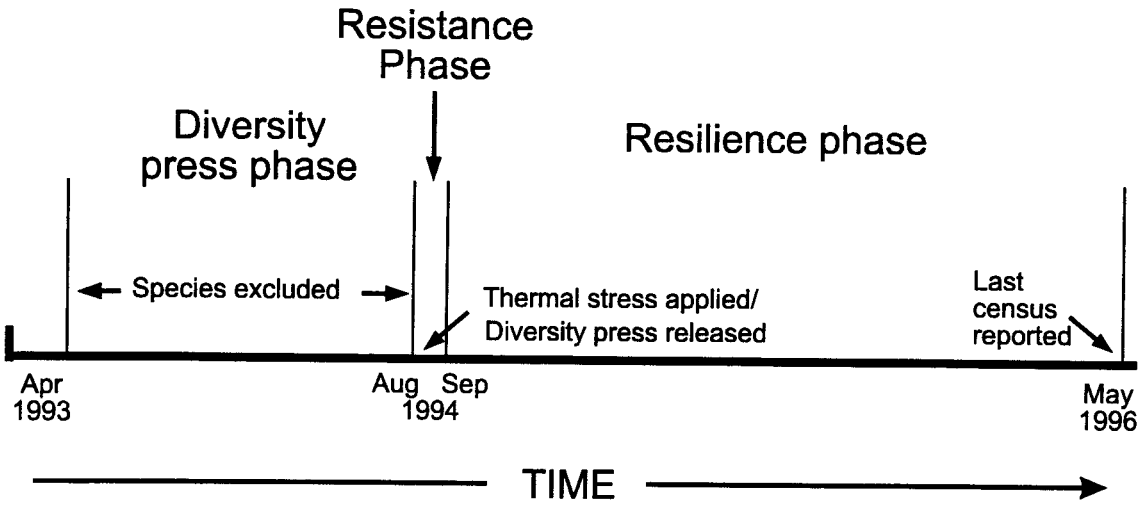

Figure 3.1. Illustration of phases of this experiment. Between April 1993 and August 1994, the diversity press was maintained by removing all excluded species from appropriate treatments. After the August 1994 census, the diversity press was released and natural recolonization of excluded species was allowed. Also, in August 1994, the thermal stress was applied to one set of plots. Resistance was estimated as the change in species and community measures from the August 1994 census to a census taken one month later. Resilience was estimated from the changes that occurred after this stress/press release.

Abundance (percent cover) of all species in two 0.25 m^2 subplots within each experimental plot was estimated in a spatially explicit manner using a grid of 256 uniform points. Sampling precision was sufficient to follow patches larger than about 40cm^2 within the subplot over time. The datum collected for each grid point was the presence of all species that intersected the point.

Stress treatment

At the end of the diversity press phase of the experiment (August 1994), one replicate from each block for each diversity treatment was randomly selected for a control group and the other replicate was used for the stress treatment group. The stress applied

to the latter group was a single-pulse thermal stress created by low-power (5000 BTU) propane heaters. One heater was suspended over each 0.25 m^2 subplot (of the 1 m^2 plots) and heat was applied for 90 minutes. Two of four subplots within each experimental plot were treated simultaneously (two heaters used) and the second set of subplots within a plot was treated immediately after the first. Because the process of applying the heat stress to all stress treatment plots took several weeks, the plot order for the heat treatment was randomized.

During normal desiccating conditions, many algal species can lose a large percentage of water and such plants typically become more resistant to heat stress (Schonbeck and Norton 1979a, Davison and Pearson 1996). This short-term "acclimation" condition can develop over the course of a few hours. To control for potential differences in plots just emersed from high tide and those emersed for several hours, I hydrated all plots scheduled to receive the heat stress during a given low tide by pouring seawater on them at regular intervals during the low tide.

Because variability in weather conditions would have seriously confounded attempts to apply a controlled temperature stress, a chamber was secured over the heated subplots to control ambient temperature and to block wind and rain. The chamber was 0.7m wide x 1.2m long x 1m high, allowing it to be placed over two subplots at a time, and was constructed of two layers of clear plastic sheeting over a frame of PVC pipe. The frame was secured to the substratum with several elastic cords attached to an anchor line (a nylon cord tied to 8-10 screws drilled into the rock around the experimental plot). The plastic sheeting on the sides of the chamber was > 1m to allow gaps between the chamber and the rock to be sealed against the wind. The propane heaters were suspended

within this chamber, 40cm above and facing the substratum. The ambient temperature within the chamber was measured with a thermometer suspended in the chamber 50cm above the substratum and was maintained below 35°C using adjustable vents constructed in the plastic sheeting. This ambient temperature rarely reached 30°C sooner than 45 minutes after the start of the stress. The heat treatment was not applied on particularly warm days.

The heaters produced a strong temperature stress. By the end of the 90 minute treatment, the surface of organisms directly under the heaters reached temperatures as high as 49°C and averaged 42°C (spot-checks measured with a digital thermometer) although temperatures under algal canopy in the same location were typically 10-15°C cooler than the surface of the canopy. Locations away from the center of the subplots were cooler: the canopy surface halfway to the edge of the subplot averaged 36°C and the surface at the edge of the subplot averaged 32°C. The temperatures in the center of the plot, although unusual, are probably not completely novel in the high intertidal of the Oregon Coast. Temperature measurements taken on August 15, 1994 at Fogarty Creek several hours after high tide recorded algal surface temperatures of over 39°C, even though ambient air temperature was 25°C. The thermal stress of this experiment, although compressed in time, produced effects similar to heat waves that occasionally occur on the coast of Oregon. For example, during the period that this stress was applied (August 1994) several days of quite warm temperatures in the intertidal coincided with midday low tides and calm wave conditions. A few areas at Fogarty Creek were apparently affected by this heat (bleaching was noted on several south facing slopes) and produced some loss of algal cover (see THERM-CONTROL in Figure 3.6).

Analysis

Although the theoretical concepts of "resistance" and "resilience" as typically defined (Orians 1975, Harrison 1979, Pimm 1991) are often employed in mathematical and simulation studies of stability, they can be difficult to make operational within an experimental context. Resistance typically means the strength or intensity of a stress that a population or community can "resist" or "absorb" without changing (Orians 1975, Underwood 1989). Empirical studies rarely are in the position to subject a community to a range of stress intensities to determine the maximum stress that causes no change. Instead, empiricists measure the magnitude of the effects of a perturbation (often at only a single level) and monitor the degree of effects (e. g., Farrell 1988, Frank and McNaughton 1991, McNaughton 1993, Tilman and Downing 1994). Comparisons of these measures are then used as surrogates for resistance.

Resilience, the inverse of the time it takes for a community to recover from a disturbance, is similarly difficult to make operational. If comparisons among treatments are to be made for resilience, this measure requires that either all treatments must recover to the reference state (a rare occurrence for natural systems within the time frame of typical experiments), or extrapolation is necessary. Such extrapolation can be impossible if patterns of recovery are highly non-linear. One compromise is to compare the proportional recovery at some time after the stress (McNaughton 1993, Tilman and Downing 1994) before all treatments have recovered. Another is to compare the patterns of community recovery after the perturbation. While these latter comparisons are not direct resilience measures (that is, measures of time), they address the same issues and

provide a wealth of detailed information on the community response to the perturbation. The analysis I present for this experiment uses a combination of these techniques to paint as clear a picture as possible of the community dynamics.

In this experiment, because the stress applied was of short duration, it was possible to decouple resistance-type dynamics (the immediate effects of stress) from resilience-type dynamics (community recovery from stress). To do so, it was necessary to control for two aspects of the pulse perturbation. To compare the magnitude of the stress effects, it is important to use comparisons in which stress intensity is similar (Connell and Sousa 1983) which is often only possible with experimentally-induced stresses. On the other hand, to measure recovery from a disturbance, it is important to compare areas that were disturbed by similar degrees. Therefore, I have partitioned the data differently for resistance and resilience analysis.

Resistance

Resistance was estimated by the magnitude of change (over one month) in species cover and community measures following the thermal stress. The primary responses for the test of resistance were the changes that occurred in dominant species cover, canopy cover, total algal cover and biomass and were calculated as:

$$\text{Absolute change} = v_{post} - v_{pre}$$

where v_{pre} was the value of the variable taken in the few days before the application of the stress and v_{post} was the value of the variable one month after the stress was applied. The post-stress census was delayed for a month to allow algae killed or bleached by the

thermal stress to slough off. Proportional change was investigated with linear regression that included v_{pre} as an independent variable in the model (see below).

To take advantage of the heat gradient created within each subplot, I partitioned the census data within each subplot into three heat-intensity levels (Figure 3.2): the area directly beneath the heaters ("HARSH"), a ring directly around that area ("INTERMEDIATE") and the remaining area of the subplot, farthest from the heaters ("MILD"). For the resistance analysis, the variables from the non-heated control plots ("THERM-CONTROL") are an average from each of these three regions in the control plots.

Besides the measure of change in individual species, three community responses were used: standing wet algal biomass (see Chapter 2 for details of its calculation); canopy cover, or the fraction of an area covered by at least one species of algae; and total algal cover, or the sum of the individual cover of all algal species in a plot. Due to layering, total algal cover can be greater than 100%.

I checked the normality of data visually with normal probability plots, box plots and the Shapiro-Wilk statistic (SAS Institute Inc. 1988). Homogeneity of variances was verified with residual plots. For the analysis of resistance, transformations of absolute change variables were not needed.

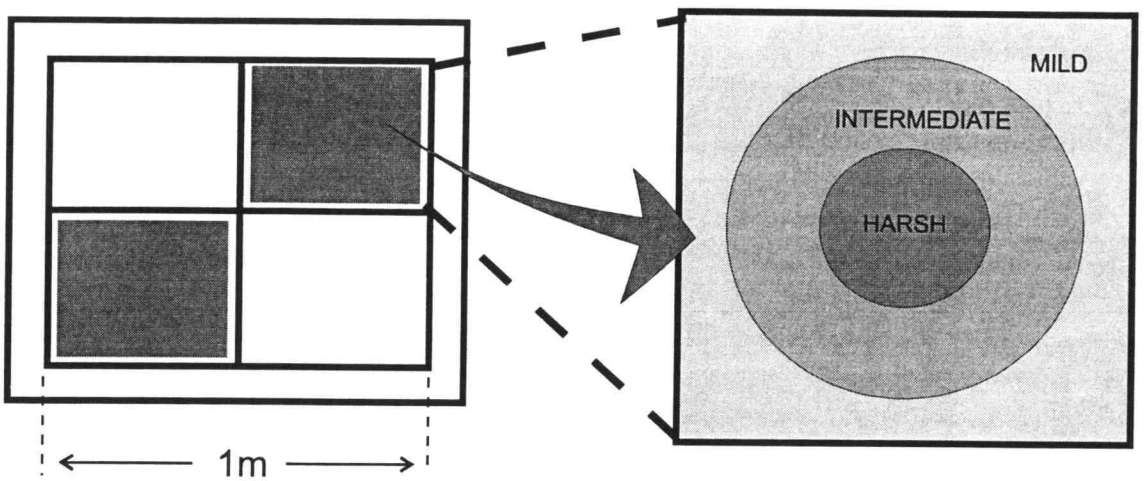

Figure 3.2. Spatial diagram of a plot and the thermal intensity pattern of the stress. The area that received the diversity manipulation included the 1 m^2 plot and buffer zone around it (left), approximately 15cm wide. Gray within plot denotes censused area (0.25 m^2). The expansion of one of these areas (right) indicates the spatial pattern of heat intensity created by propane heaters. This pattern was replicated in all four 0.25 m^2 subplots. HARSH, INTERMEDIATE, and MILD indicate the partition zones for the "resistance" data sets. Each zone is treated separately in the analysis.

To test for resistance differences among diversity treatments, I performed MANOVA on the absolute change in community and species measures. Although a full MANOVA model that included all dependent variables would have been desirable to account for covariance among dependent variables (Littell et al. 1991, Scheiner 1993), such an analysis was not possible because several species variables were explicitly manipulated in some treatments. For example, in the analysis of Mastocarpus, a foliose red, it would not be appropriate to include treatments where foliose reds were excluded. As a compromise, therefore, I performed separate MANOVA analyses on four groups of related variables (community variables; barnacles, fucoids, and foliose-red algae).

Because heat levels (HARSH, INTERMEDIATE, and MILD) within each subplot were spatially correlated, I could not treat them as independent levels due to potential inflation of p-values (Kenny and Judd 1986). Therefore, when comparisons were made to non-heated controls, I performed separate analyses on each heat level compared to the controls and adjusted the p-values for multiple comparisons using the Dunn-Sidák method (Sokal and Rohlf 1981). When comparisons were not made to the control plots, I performed separate analyses on each heat level but did not adjust the p-value. Similar precautions were taken with the resilience analysis.

To identify the factors that best explained the variation in resistance, I performed a series of stepwise multiple regressions on the change of each response variable at each heat level. The potential predictor (i. e., independent) variables included in the full model were pre-stress measures of: 1) diversity (total number of species, number of algal groups, and average point diversity defined as average number of species that intersect each grid point), 2) abundance of other dominant species in the plot, 3) community variables (i. e., canopy cover, total algal cover, and biomass; these were used only for regressions of species change and were not included in regressions in which another community measure was the dependent variable), and 4) physical characteristics of subplots (substratum angle, emersion index; see Chapter 2). The pre-stress value of the dependent variable (v_{pre}) was forced into each regression model as an independent variable. Initial runs of these regressions demonstrated that these pre-stress variables were strongly significant in almost all regressions (exceptions were MILD: Endocladia; INTERMEDIATE: canopy, Balanus).

Resilience

For the resilience analysis, I partitioned the data somewhat differently. Because resilience to a disturbance that removed most or all of the resident biomass could be different from a less catastrophic disturbance, I compared areas that were similarly disturbed by separately following recovery in two types of areas within the thermally-stressed plots. For the "SEVERE" level, I included just those areas within a subplot that experienced a dramatic change in cover. These areas satisfied the following criteria: 1) a census grid point was included in the area if it had been occupied by an organism for the two censuses before the thermal stress, but was unoccupied after the stress, 2) it was contiguous with at least two other such points, 3) the set of these grid points was at least 40 in number ($\approx$400cm^2) and 4) 90% of the grid points within the perimeter of the selected area were bare after the stress. Thus, these areas (SEVERE) were highly disturbed space. By these criteria, some subplots were excluded from the SEVERE data set either because pre-stress cover in the central area was not high enough to create a contiguous patch of high change or because the clearances created by the stress were too small and patchy. The size of these selected areas was not significantly different among treatments ($F_{8,28} = 1.23$; $P = 0.3$; average=722cm^2, SE=34.5, n=37). The second data set in the thermally-stressed plots (termed "MODERATE"; average size = 1720cm^2, SE=29.6, n=50) excluded all grid points that occurred in the SEVERE data set or in the HARSH data set (as defined in the resistance analysis). This level thus received an intermediate level of disturbance. The plots that did not receive the heat stress but did receive the diversity press ("THERM-CONTROL") were also analyzed. The differences

between the spatial partitions used in resilience and resistance analysis are summarized in Table 3.2 and Figure 3.3.

Table 3.2. Comparison of the resistance and resilience data sets. Subplots within the heat stressed plots were spatially partitioned in the resistance data set by characteristics of the physical stress (heat intensity) and in the resilience data set by characteristics of level of disturbance created by the thermal stress.

RESISTANCE		**RESILIENCE**	
All plots were partitioned in the same manner because the heaters were placed in the same spatial position.		Areas of severe disturbance were defined individually for each subplot depending on the degree of disturbance.	
PARTITION NAME	DEFINITION	PARTITION NAME	DEFINITION
HARSH	Central grid points of a subplot over which heater was placed.	SEVERE	Areas within subplot that lost substantial cover and were of a sufficient contiguous size.
INTERMEDIATE	Ring surrounding central area of the subplot.	MODERATE	Areas that were not included in the SEVERE data set and were not in the central ring that had received the strongest heat stress.
MILD	Areas within the subplot that were farthest from the heaters.		

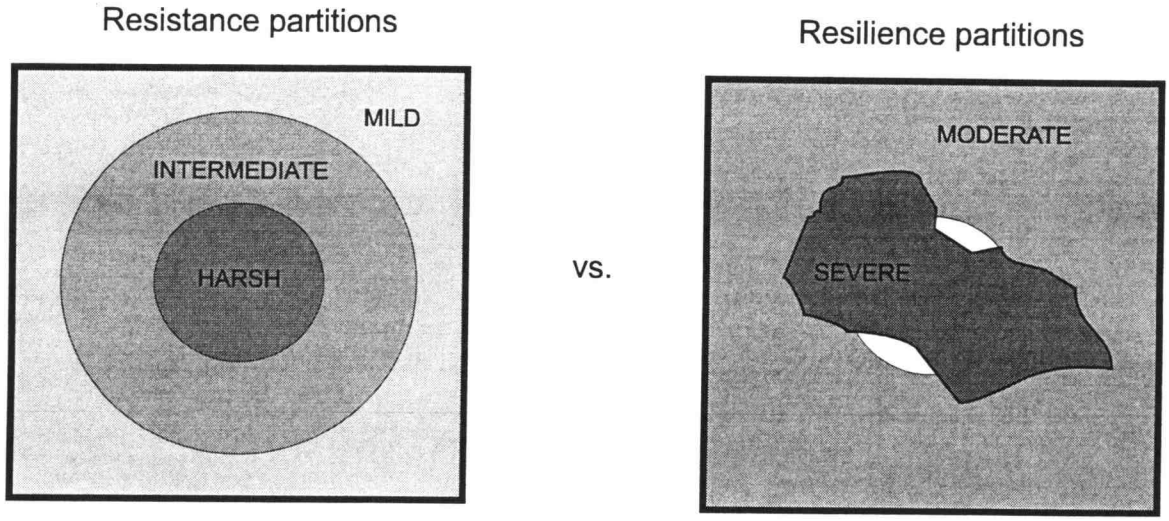

Figure 3.3. Illustration of the difference between resistance and resilience partitions of the plots that received the thermal stress. White areas in resilience partitions are not included in the data sets of either SEVERE (because they did not meet the criteria) or MODERATE (because they had received the HARSH stress).

Although resilience is usually defined as a measure of the speed of recovery (Orians 1975, Harrison 1979, Pimm 1984), such calculation requires either completion of recovery (i. e., disturbed plots become indistinguishable from the references) or extrapolation of the time it takes to reach such states. By November 1996, (26 months after the thermal stress) many plots were still quite different from the reference plots and, therefore, direct calculation of recovery times was not possible. Further, because of the non-linear progression of recovery, extrapolation was not possible without highly subjective judgments about the course of succession. Thus, to explore the resilience to the thermal stress, I used three alternative types of analysis: first, I quantified community "trajectory" with ordination techniques that reduced the multivariate community response to a few axes of dominant variation. Second, I classified experimental subplots into discrete community "states" and compared the patterns of recovery among diversity

treatments and disturbance levels. Third, I calculated the proportional recovery of standing algal biomass in the last census of the recovery period to a reference level. The need for data transformations was evaluated in the same manner as for the resistance data sets. The transformations performed on variables for resilience analysis are listed in the captions of the analysis tables and satisfactorily removed deviations from analysis assumptions.

Reference plots

Most proposed measures of resilience are based on comparisons of the perturbed community to some reference state or value. This reference may be a calculated "equilibrium" value (Pimm 1991), the value of the community before the perturbation (Tilman and Downing 1994) or an area that remains non-manipulated throughout the experiment (McNaughton 1985, 1993). In this study, a set of 15 $1m^2$ reference plots was used for comparisons. These plots were among the original pool of plots from which the diversity treatments were randomly selected. Thus, these plots are representative of the conditions and composition of the experimental plots with no manipulation (both diversity and stress manipulation). For some resilience comparisons below (biomass recovery and principal components analysis), all censuses for a given reference plot were averaged. For other comparisons, several censuses of each reference plot were used to illustrate the typical dynamics among non-manipulated experimental plots throughout the entire experiment (see "Community states").

Patterns of community recovery

I used principal components analysis (PCA) to compare the broad community differences between diversity treatments and disturbance levels. Each ordination includes the reference plots as well as all treatments within a disturbance level for a given date. The variables used in this analysis were measures of standing algal biomass (wet), species richness, and the cover of canopy, fucoids, foliose reds, low abundance algal species, and barnacles. To adjust for variables of different scales, all values were rescaled by relativizing to the variable's maximum (see McCune and Mefford 1995). Ordinations were performed using PC-ORD (McCune and Mefford 1995) and the variance explained by each displayed axis was tabulated.

Community states

The effects of the disturbance level and the diversity treatments on resilience were further explored by identifying the major community states that occurred across the experiment and classifying all experimental units to one of these states at several time points throughout the resilience period. As such, this analysis summarizes very complex data into ecologically relevant categories and yields a direct visual result to allow comparisons of dominant patterns.

To identify the major community states that occurred within this experiment, first a dendrogram was generated using the data from all treatments at several census dates to capture the range of composition variability within the experiment. The data used in this

cluster analysis were proportional cover of all species whose abundance was greater than 10% in at least 10% of the plots (Fucus, Pelvetiopsis, Mastocarpus, Mazzaella, Endocladia, Cladophora, Balanus, Chthamalus). These data were rescaled to equalize the maximum abundance of all species. The clustering used Euclidean distance and Ward's group linkage method (see McCune and Mefford (1995) for a description of these methods). The clustering was performed in PC-ORD (McCune and Mefford 1995). The generated dendrogram was then used to identify the major groupings in the entire set. I collapsed some of the eleven major groupings into a single "state." For example, I collapsed the three groupings identified by the clustering, Mastocarpus-dominated, Mazzaella-dominated, and Mastocarpus + Mazzaella-dominated, into the single state "foliose-red dominated." Using these groupings, I developed a set of numeric criteria to classify all dates of all treatments into one of 6 states (Table 3.3) and the characters of the states are described as follows:

•Bare rock-dominated: these areas were either completely bare or had sparse cover of sessile organisms. Small patches of bare-rock are often heavily grazed by limpets (Farrell 1989, Kim and DeWreede 1996). Such patches are usually quickly colonized by barnacles or ephemeral algae.

•Barnacle-dominated: this is a typical early successional stage after free space is created. In these areas, high cover of barnacles can reduce grazing by limpets and can also serve as recruitment substrate for several species (e. g., Endocladia, fucoids) (Dayton 1971, Farrell 1991).

Table 3.3. Community "states" and criteria for classification. State classification is progressive, that is, states on the bottom of the list are assigned only if the criteria for the states above it are not met. All criteria are measures of cover: "TotAlg" is the additive cover of all algal species, "Barnacle" is the cover of Balanus, Chthamalus, Semibalanus cariosus and Pollicipes polymerus. The few experimental units that were not classified by this scheme were evaluated individually; most were of sparse algal cover and were put into the "rock" state.

State	Code used in Figures	Criteria
Rock-dominated	R	TotAlg < 0.3 Barnacle < 0.3
Barnacle-dominated	B	TotAlg < 0.3 Barnacle > 0.3
Balanus/Endocladia dominated	B/E	Balanus > 0.4 Endocladia > 0.3 Total non-Endocladia algae < 0.3
Cladophora dominated	C	Cladophora > 0.4
Foliose red dominated	FR	(Mastocarpus > 0.4 or Mazzaella > 0.4 or (Mastocarpus + Mazzaella) > 0.6) AND (Mastocarpus + Mazzaella) > fucoid
Fucoid dominated	F	Fucoid > 0.4

•Balanus/Endocladia-dominated: while common in rocky intertidal areas of the NE Pacific (Glynn 1965), often as a late successional state, this state was not prevalent as such in the experimental areas. More often, plots in this state were either colonized by fucoids or, in areas of dense Endocladia mats, barnacles were smothered by Endocladia and eventually sloughed off the rock leaving a rock-dominated area (G. Allison, personal observation).

•Fucoid-dominated: this was the most prevalent state within this experiment and is very common in many high intertidal communities (Dayton 1971, Farrell 1991, Chapman 1995). In more wave-protected areas, fucoids can develop a heavy canopy which may subject other organisms to reduced light, potential whiplash effects (Dayton 1971, Kim and DeWreede 1996) but also may potentially reduce desiccation stress for organisms under the canopy.

•Foliose red-dominated: when Mastocarpus and Mazzaella are abundant in plots, the plants often have a dense cluster of blades and can dominate primary space with thick crusts and dense holdfasts (Hay 1981, Olson 1992, G. Allison, personal observations). While fucoids can be present in such areas, fucoid recruits occur mostly at edges of Mazzaella patches and outside of dense Mastocarpus patches.

•Cladophora-dominated: these states are often seasonal as Cladophora is most abundant in spring and summer. Because the species creates a dense mat, it can smother other organisms, especially barnacles. Although commonly found at Fogarty Creek in low abundance, Cladophora usually only occurs in high abundance under fairly specific physical conditions: relatively flat substratum where drainage at low tide is slow or is near constant sources of water such as shallow pools or slowly draining channels. Other algal species co-occur in Cladophora-dominated plots though rarely within the Cladophora mat.

Biomass recovery

I calculated the recovery to reference levels of standing algal biomass in the last census of the recovery period (May 1996; 21 months after the thermal stress and release of the diversity press). This was calculated in a manner similar to Tilman and Downing (1994) by comparisons to the average biomass in reference plots. ANOVA was used to test for disturbance level effects and diversity treatment effects.

RESULTS

Immediate effects of the thermal stress

The application of the thermal stress to each subplot produced intense heat in the center of the subplot, decreasing toward the edges. This stress usually produced considerable mortality and/or tissue damage to sessile and mobile species in the center, but much less so away from the center (Figure 3.4). Algal bleaching usually took at least 24 hours and bleached algae typically took one to three weeks to slough off from the remaining live plant tissue or from the rock. The shells of the barnacles Balanus and Chthamalus killed by the stress remained on the rocks for longer, but most had been dislodged within six weeks. Although mobile species such as limpets, littorines and amphipods were often killed in the center of the subplots by the heat, the areas were usually recolonized by these groups in just a few days.

The net result of the stress on the community, although intense, was similar to natural disturbances. Natural heat and/or desiccation stress can produce very similar results when they cause plant tissue damage, bleaching, and therefore reduction of cover of both species and total canopy (Emerson and Zedler 1978, Hay 1981, Taylor and Littler 1982, Olson 1985, Bell 1993, Chapman 1995, Davison and Pearson 1996). Other natural disturbances such as logs or rocks rolling in the surf may be more severe (Dayton 1971, Paine and Levin 1981, Sousa 1985). The force applied by such disturbance can remove most organisms in the impact area. Each of these disturbances is common in the rocky intertidal of Oregon and produces effects similar to what was seen here: reduction in cover or complete removal of organisms from the rock.

Resistance

The thermal stress affected virtually all response variables (Figure 3.5-3.8). Absolute change in the stressed plots was particularly strong in the HARSH zones. By the definition of resistance as the level of perturbation that the community can resist without change, all heat stress levels overcame the community resistance (Table 3.4; STRESS is significant in almost all variables).

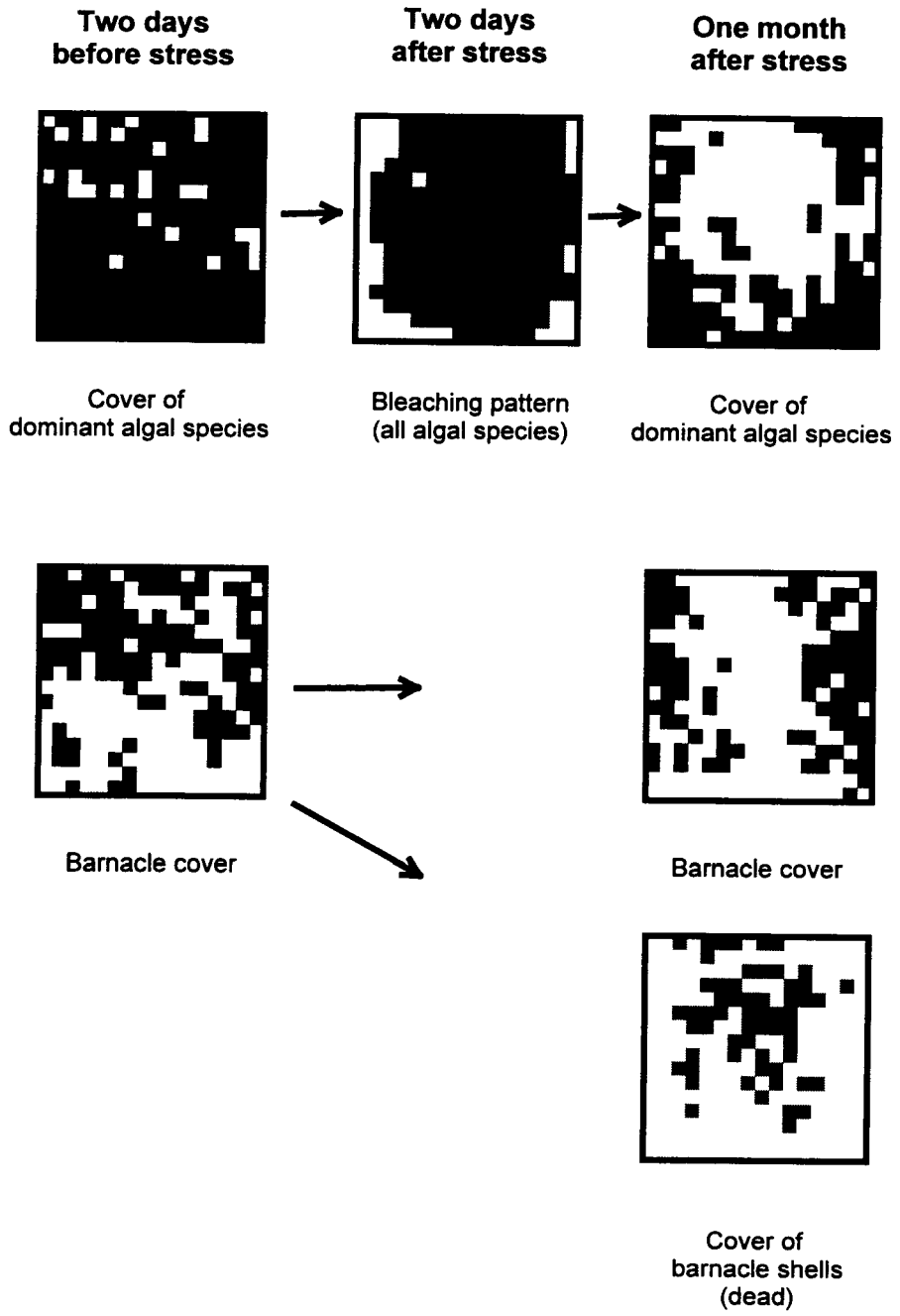

Figure 3.4. Example of the immediate effects of the thermal stress on an experimental subplot. Spatially explicit illustration of the condition of each point on the grid of 256 points for one high diversity (+F+R+M) subplot. Each filled cell represents the presence of the displayed character (e. g., barnacle, dominant algae). Dominant algal species include Fucus, Pelvetiopsis, Mazzaella and Mastocarpus. Barnacle species include Balanus and Chthamalus. Bleaching pattern indicates all the points on the grid that intersected an alga that were visibly damaged after the thermal stress.

Responses to diversity treatments were also strong (Table 3.4). In particular, the community variables (standing algal biomass, canopy cover, and total algal cover, analyzed together) exhibited both TRT effects for all heat levels and TRTxSTRESS interaction in the HARSH level (Table 3.4A) suggesting that some diversity treatments were more affected by the stress. For total algal cover and canopy cover, the two low diversity treatments (L1, L2) were the least affected (Figure 3.5). In the case of the standing algal biomass, treatments most strongly affected were those with fucoids and especially the high and mid diversity treatments (H, M2). As I illustrate below, these treatment differences were highly correlated with the initial amounts of biomass, total algal and canopy cover. Thus, the primary direct effect of the stress was the reduction of cover and, for the community variables, the higher diversity treatments were affected the greatest.

Figure 3.5. Resistance: absolute change ($v_{post}-v_{pre}$) in cover of community variables due to thermal stress. Error bars are standard errors (n=5).

Figure 3.6. Resistance: absolute change ($v_{post}-v_{pre}$) in cover of foliose red species due to thermal stress. Only diversity treatments that did not exclude foliose red species are shown. '+' indicates treatments in which fucoids were included. Error bars are standard errors (n=5).

Figure 3.7. Resistance: absolute change ($v_{post}-v_{pre}$) in cover of fucoids due to thermal stress. Only diversity treatments that did not exclude fucoids are shown. Error bars are standard errors (n=5).

Figure 3.8. Resistance: absolute change ($v_{post}-v_{pre}$) in cover of barnacles due to thermal stress. Error bars are standard errors (n=5).

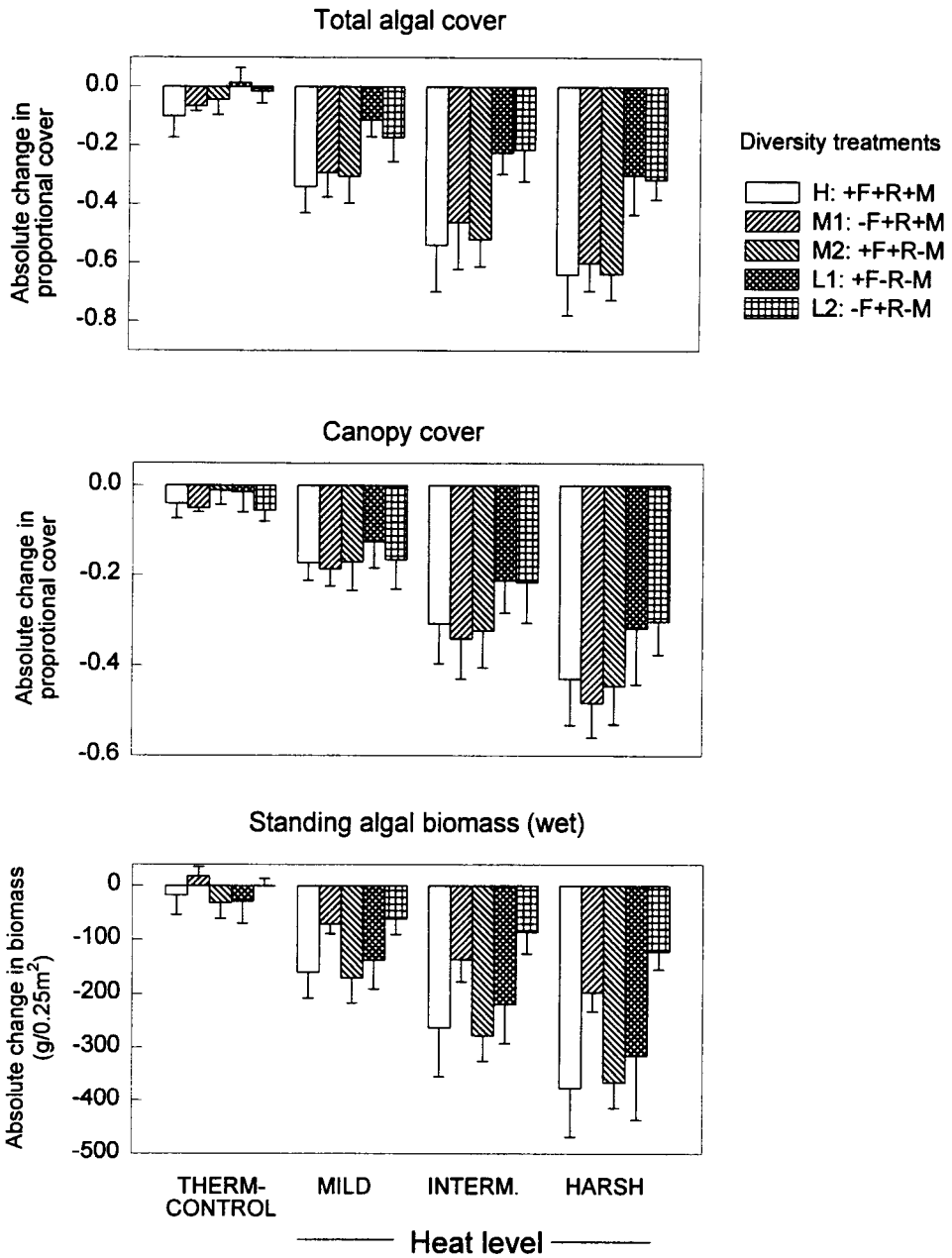
Total algal cover
Absolute change in proportional cover
0.0
-0.2
-0.4
-0.6
-0.8
Diversity treatments
H: +F+R+M
M1: -F+R+M
M2: +F+R-M
L1: +F-R-M
L2: -F+R-M
Canopy cover
Absolute change in proprotional cover
0.0
-0.2
-0.4
-0.6
Standing algal biomass (wet)
Absolute change in biomass (g/0.25m2)
0
-100
-200
-300
-400
-500
THERM-CONTROL
MILD
INTERM.
HARSH
Heat level

Figure 3.5

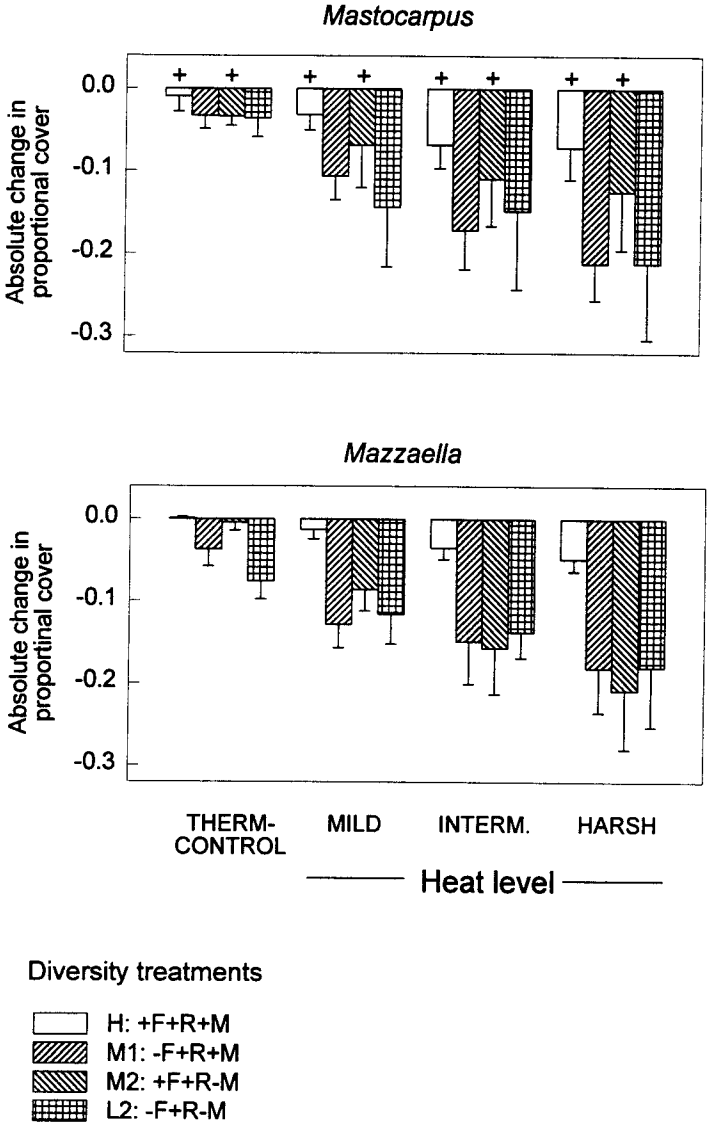
Mastocarpus
Absolute change in proportional cover
0.0
-0.1
-0.2
-0.3
Mazzaella
Absolute change in proportinal cover
0.0
-0.1
-0.2
-0.3
THERM-CONTROL
MILD
INTERM.
HARSH
Heat level
Diversity treatments
H: +F+R+M
M1: -F+R+M
M2: +F+R-M
L2: -F+R-M

Figure 3.6

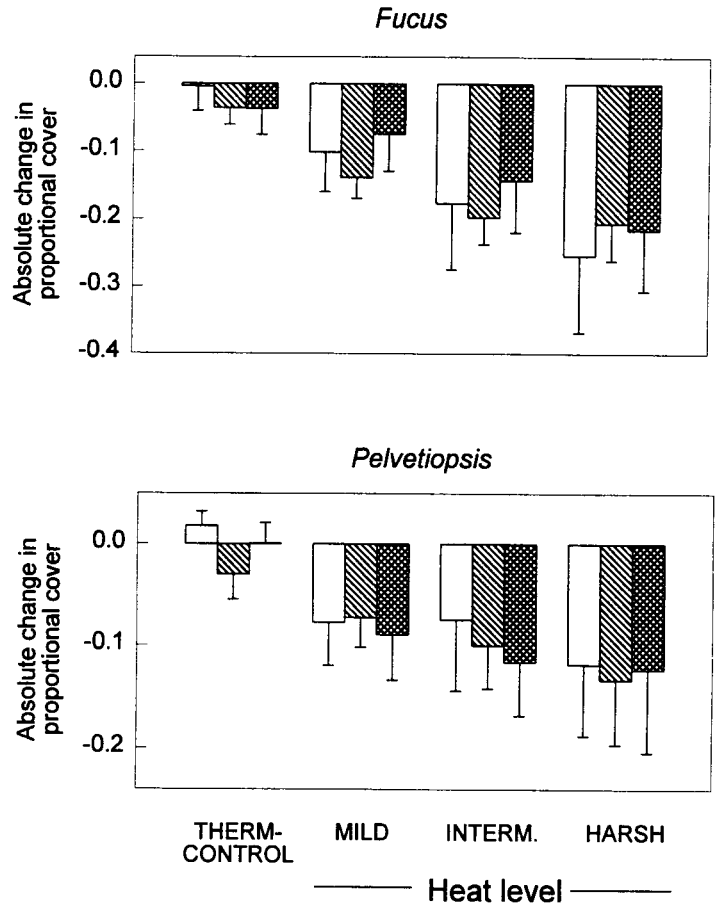
Fucus
Absolute change in proportional cover
0.0
-0.1
-0.2
-0.3
-0.4
Pelvetiopsis
Absolute change in proportional cover
0.0
-0.1
-0.2
THERM-CONTROL
MILD
INTERM.
HARSH
Heat level
Diversity treatments
H: +F+R+M
M2: +F+R-M
L1: +F-R-M

Figure 3.7

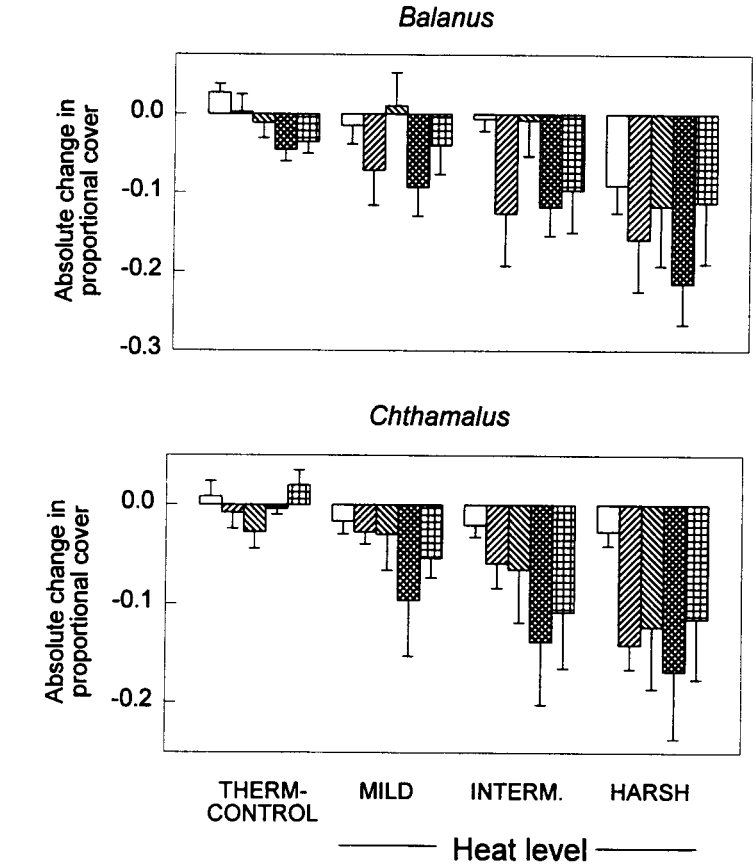
Balanus
Absolute change in proportional cover
0.0
-0.1
-0.2
-0.3
Chthamalus
Absolute change in proportional cover
0.0
-0.1
-0.2
THERM-CONTROL
MILD
INTERM.
HARSH
Heat level
Diversity treatments
H: +F+R+M
M1: -F+R+M
M2: +F+R-M
L1: +F-R-M
L2: -F+R-M

Figure 3.8

Table 3.4. MANOVA analysis of resistance to thermal stress. Of each set of variables (A-D), 3 MANOVAs were performed comparing one thermal stress level to the controls. Because of this multiple comparison to controls, significance was adjusted by the Dunn-Sidák criteria ($\alpha = 0.05$ at $p < 0.0169$) and boldface type indicates a significant effect. Ndf = numerator degrees of freedom, Ddf = denominator degrees of freedom, Wλ = Wilks' lambda statistic. TRT = diversity treatment effect; STRESS = thermal stress effect; BLK = block effect.

A. Community data

			MILD			INTERMEDIATE			HARSH		
Source	Ndf	Ddf	W λ	F	P	W λ	F	P	W λ	F	P
STRESS	3	42	0.556	11.1	**0.0001**	0.385	22.4	**0.0001**	0.282	35.7	**0.0001**
TRT	15	116	0.182	6.63	**0.0001**	0.175	6.81	**0.0001**	0.160	7.31	**0.0001**
TRTx STRESS	15	116	0.777	0.742	0.7373	0.618	1.48	0.1257	0.467	2.46	**0.0037**
BLK	12	111	0.545	2.39	**0.0087**	0.558	2.229	**0.0120**	0.667	0.154	0.1213

B. Foliose red data

			MILD			INTERMEDIATE			HARSH		
Source	Ndf	Ddf	W λ	F	P	W λ	F	P	W λ	F	P
STRESS	2	35	0.576	12.9	**0.0001**	0.489	18.3	**0.0001**	0.326	36.1	**0.0001**
TRT	8	70	0.483	3.83	**0.0009**	0.683	1.83	0.0856	0.633	2.25	0.0336
TRTx STRESS	8	70	0.779	1.17	0.3291	0.839	0.800	0.6044	0.812	0.963	0.4717
BLK	8	70	0.659	2.03	0.0556	0.700	1.71	0.1124	0.696	1.74	0.1040

C. Fucoid data

			MILD			INTERMEDIATE			HARSH		
Source	Ndf	Ddf	W λ	F	P	W λ	F	P	W λ	F	P
STRESS	2	27	0.566	10.3	**0.0005**	0.373	22.7	**0.0001**	0.359	21.5	**0.0001**
TRT	6	54	0.935	0.308	0.9300	0.874	0.679	0.7065	0.956	0.207	0.9732
TRTx STRESS	6	54	0.916	0.403	0.8738	0.950	0.234	0.9637	0.963	0.170	0.9837
BLK	8	54	0.414	3.73	**0.0015**	0.403	3.88	**0.0011**	0.462	3.18	**0.0050**

Table 3.4 Continued

D. Barnacles data

			MILD			INTERMEDIATE			HARSH		
Source	Ndf	Ddf	W λ	F	P	W λ	F	P	W λ	F	P
STRESS	2	43	0.831	4.38	0.0185	0.760	6.77	**0.0028**	0.600	14.3	**0.0001**
TRT	10	86	0.731	1.46	0.1699	0.680	1.82	0.0677	0.648	2.08	0.0345
TRTx STRESS	10	86	0.797	1.03	0.4218	0.754	1.30	0.2430	0.751	1.33	0.2297
BLK	8	86	0.808	1.21	0.3030	0.814	1.16	0.3306	0.745	1.70	0.1095

A few other direct effects of thermal stress were notable. There was a TRT effect in the MILD stress on the foliose red algal species (Mastocarpus and Mazzaella; Table 3.4B). This effect was most likely attributable to the presence or absence of the fucoid group: the change in Mastocarpus (Figure 3.6) in treatments where fucoids were present (H and M2; bars marked with '+') was much less than in treatments in which fucoids were absent (M1 and L2). This is again attributable to more loss in treatments with higher cover: exclusion of fucoids released Mastocarpus from competition and allowed an increase in abundance (see Chapter 2 for a description of the difference among treatments for Mastocarpus). Also, block differences were detected in the community variables and the fucoids suggesting spatial variability in the effect. However, although there were clearly thermal stress effects in the fucoids (Figure 3.7) there were no significant diversity treatment effects (Table 3.4C). The situation was similar for barnacles (Figure 3.8) although there was a marginally non-significant TRT effect in the INTERMEDIATE and HARSH zones (Table 3.4D), due to the low loss of Chthamalus in the high diversity treatment.

Multiple regression

Multiple regression was used to identify the primary predictors for the variation in the effects of the stress. By far, the dominant predictor for the change in a given response variable was the pre-stress value of the variable (Figure 3.9; open portion of bars) and in general, this predictor explained more of the variation at higher thermal stress levels. Furthermore, the regression coefficient for this predictor in all regression models was negative, meaning that larger initial values were strongly correlated with larger reductions in abundance. That is, the greatest losses from thermal stress were in those areas with the most to lose.

Diversity explained some of the variation in barnacle and canopy cover (Figure 3.9, solid portion of bars). For these measures in which diversity was selected as a significant predictor, the significant aspect of diversity was point diversity or the average number of species under each point of the census grid. Further, the regression coefficient for this predictor was, in all cases, positive (not shown in figure), meaning that there was a smaller loss at high point diversity. This point diversity effect found for Balanus (MILD) was probably just a reflection of less change in areas of lower abundance: low Balanus cover was associated with high point diversity ($p<0.0012$;$R^2=10\%$ for the census taken before the heat stress). However, because there was a strong direct correlation between high point diversity and high canopy cover ($p<0.0001$; $R^2=76\%$), the positive diversity coefficient suggests that high point diversity in some way ameliorates the severity of the stress. That is, although areas with high canopy were strongly affected, high canopy areas with high point diversity were less severely effected.

Figure 3.9. Stepwise linear regression results on absolute change (v_{post}–v_{pre}). Each bar represents the results of a single regression: the dependent variable (listed on the x-axis) was the absolute change in the variable due to thermal stress. See Methods for list of independent variables used in regression. Each portion of the stacked bar represents the partial correlation coefficient for the independent variable found by the stepwise procedure to be significant ($\alpha = 0.05$), that is, the percentage of the variation explained in the dependent variable. All appropriate treatments were included (e. g., fucoid exclusion treatments were not used for the analysis of Fucus resistance).

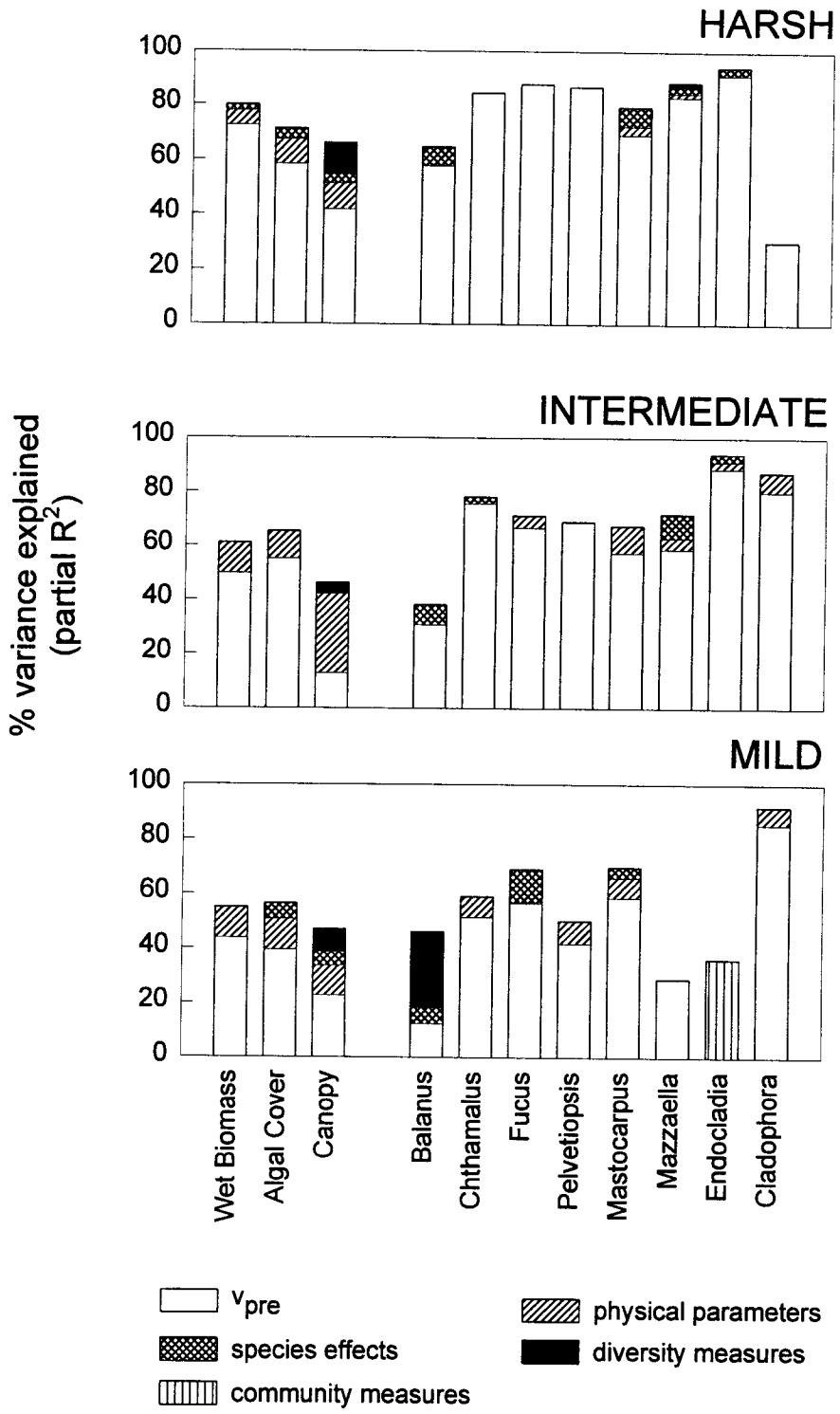
HARSH
INTERMEDIATE
MILD
% variance explained (partial R^2)
100
80
60
40
20
0
Wet Biomass
Algal Cover
Canopy
Balanus
Chthamalus
Fucus
Pelvetiopsis
Mastocarpus
Mazzaella
Endocladia
Cladophora
v_{pre}
species effects
community measures
physical parameters
diversity measures

Figure 3.9

Measures of desiccation potential also explained some of the variation in the thermal effect (Figure 3.9; slanted fill). The regression coefficients for these significant variables were all positive, suggesting that the areas that are normally under higher desiccation stress were less affected by thermal stress. This is likely because the experimental stress was applied uniformly across the desiccation gradient. Organisms on the upper edge of this gradient, exposed to more desiccation stress naturally, probably had been selected by previous stresses (Schonbeck and Norton 1979a).

There was little difference in the relative effect of high temperature on the four dominant algal species (Table 3.5, Figure 3.10). Although there was some suggestion that there was a species difference between the MILD heat level and the controls in how Mastocarpus vs. Pelvetiopsis responded to the stress, this trend was not significant. For the most part, the thermal stress was non-selective: no one species was strongly affected whereas another species was only weakly affected (no SPECIES or SPECIESxSTRESS effects; Table 3.5).

Table 3.5. ANOVA results for proportional change to thermal stress among major species: Fucus, Pelvetiopsis, Mazzaella and Mastocarpus. Each test (MILD INTERMEDIATE and HARSH) is a comparison of the stressed areas to the control areas with the four species as a class effect. Because of the multiple comparisons to the control plots, criteria for significance is by Dunn-Sidák criteria ($\alpha = 0.05$ at $p < 0.0169$) and the boldface type indicates a significant effect.

		MILD			INTERMEDIATE			HARSH		
Source	df	MS	F	P	MS	F	P	MS	F	P
STRESS	1	2.07	22.35	**0.0001**	5.743	72.9	**0.0001**	7.75	68.6	**0.0001**
SPECIES	3	0.266	2.87	0.0379	0.159	2.02	0.1130	0.154	1.36	0.2550
SPECIESx STRESS	3	0.239	2.57	0.0559	0.158	2.00	0.1150	0.276	2.44	0.0656
BLK	4	0.278	2.99	0.0201	0.350	4.44	**0.0019**	0.214	1.90	0.1125
Error	184	0.0929			0.0787			0.113		

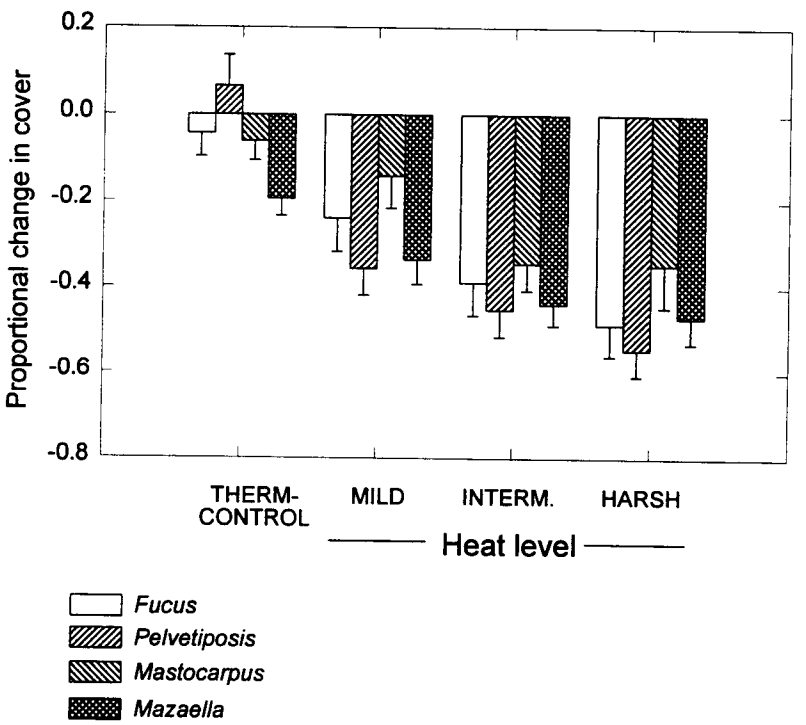

Figure 3.10. Relative sensitivity to thermal stress for algal major species. Proportional change in cover, using all treatments in which the species was not excluded.

Resilience

After the thermal stress was applied, the diversity press was released. This aspect of the experiment allowed examination of the effect of disturbance level on recovery as well as how differences in diversity affected that recovery. Comparison of high diversity treatments (all species present) for different disturbance levels addresses how this community recovers from a stress to its pre-stress condition; comparisons of reduced diversity treatments to reference states should indicate both how the degree of disturbance and the initial "deviation" from the reference influences recovery to that reference.

Ordinations

As described above and in detail in Chapter 2, before the thermal stress was applied, the diversity press was maintained for 15 months. Prior to this press, most plots in this experiment were roughly within the range of variation that occurred among reference plots (Figure 3.11A). However, by the end of the diversity press (August 1994) the plots in several treatments (M1:-F+R+M, L1:+F-R-M, L2:-F+R-M; Figure 3.11B) clustered far from the reference and the variation among these different treatments was far greater than that among reference plots. However, the high diversity treatment (H: +F+R+M) as well as several plots of the mid-diversity treatment (M2: +F+R-M) clustered within the reference set.

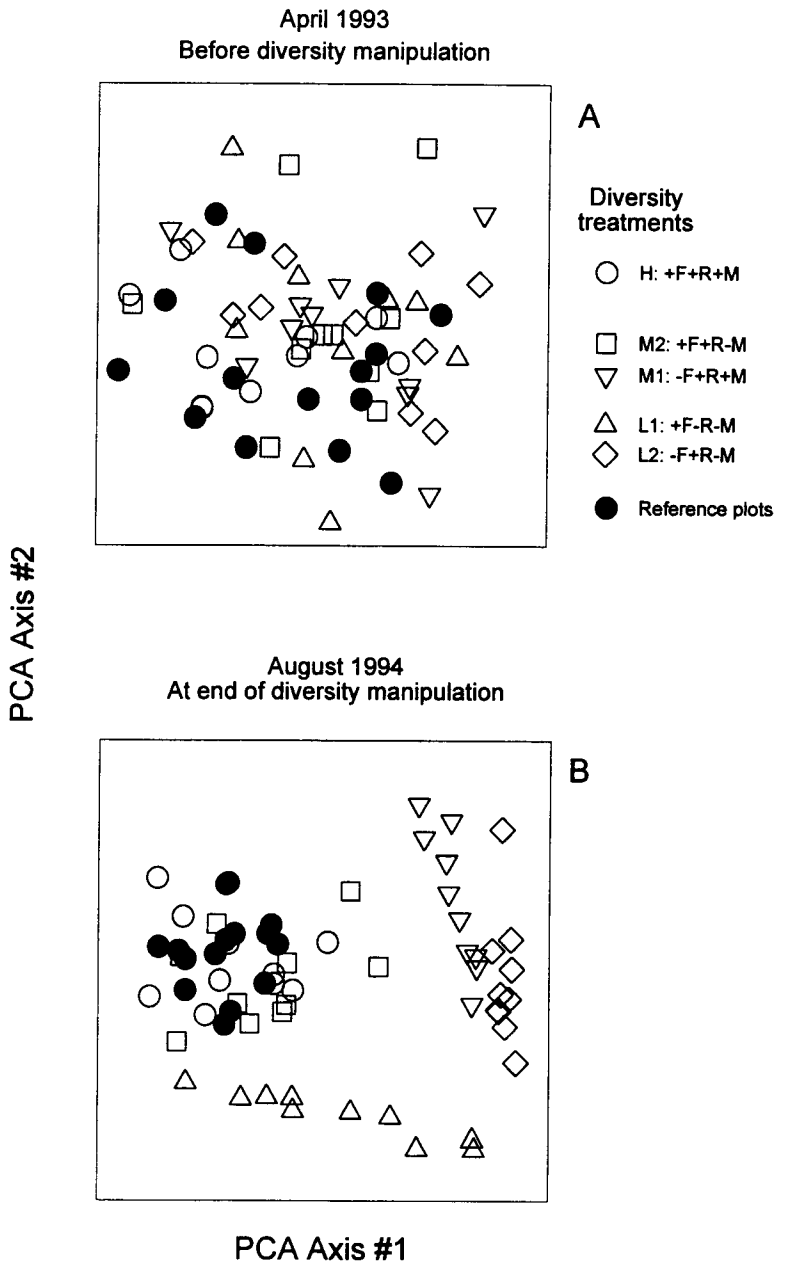

Figure 3.11. Principal components analysis of plots before the diversity manipulation and before the stress was applied. PCA performed on measures of ln(biomass), total algal cover, and plot species richness, and the arcsin squareroot transform of barnacle cover, fucoid cover, foliose red cover, low abundance species cover. Values for the reference plots were the average of all censuses. See Table 3.6 for percent variance explained by each axis.

The extensive effects of the heat treatment in the highly disturbed areas (SEVERE) were clear in the community ordinations (compare Figure 3.12A,B to Figure 3.12C). The differences among treatments, evident just one month before (Figure 3.11B) were essentially removed by the disturbance. Further, none of the stressed plots were similar to reference plots and there was more variation among the reference plots than among disturbed plots (Figure 3.12C). Over the next 21 months, these disturbed areas gradually diverged (Figure 3.12C, F, I). Yet, by the end of that period only a few plots were similar to the reference plots (Figure 3.12I).

The MODERATE disturbed plots showed lesser effects, but differences from THERM-CONTROLs were still evident (Figure 3.12). Immediately after the stress, few of the stressed treatments were similar to (that is, clustered with) the reference plots (Figure 3.12B), unlike the THERM-CONTROL plots (Figure 3.12A). After 21 months, many of the THERM-CONTROL plots had become similar to the reference plots although several of L1, M1 and L2 plots were still outside of the reference cluster (Figure 3.12G). But for the MODERATE treatment, many more plots were outside of the reference cluster and the total variation across all plots was still much greater than among the reference plots (Figure 3.12B, E, H).

Table 3.6. Percent variation explained in principle components analysis. Table includes the percent variation explained on both axes in each graph in Figures 3.11 and 3.12. Also included are the number of axes from the analyses that are interpretable or "significant" by the broken-stick criteria (Jackson 1993, McCune and Mefford 1995).

Figure	Percent variation explained by AXIS #1	Percent variation explained by AXIS #2	Number of significant axes
Figure 3.11 A	41.5	25.6	3
Figure 3.11 B	45.6	33.7	2
Figure 3.12 A	45.9	33.6	2
Figure 3.12 B	54.5	24.7	2
Figure 3.12 C	84.6	6.1	1
Figure 3.12 D	46.9	30.0	2
Figure 3.12 E	52.1	24.9	2
Figure 3.12 F	73.1	10.0	1
Figure 3.12 G	44.9	28.3	2
Figure 3.12 H	47.0	31.1	2
Figure 3.12 I	72.8	12.9	1

Figure 3.12. Principal components analysis (PCA) of the community trajectory for three stress levels: THERM-CONTROL, MODERATE, SEVERE. See Figure 3.11 for more details. Note that the axes for each ordination are not necessarily the same. Because the reference values are the same in all ordinations, those reference values can be used to judge the variance among all plots.

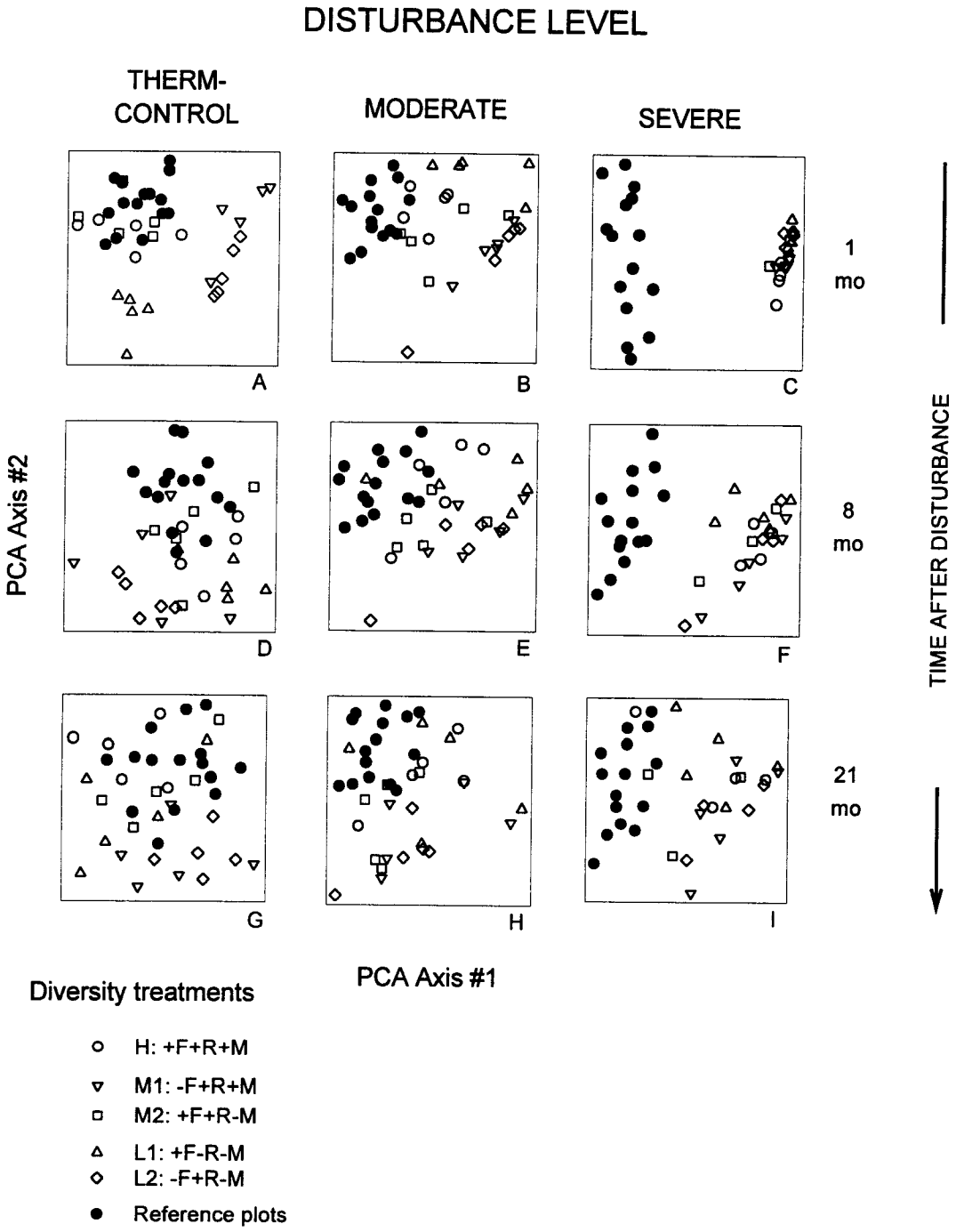
DISTURBANCE LEVEL
THERM-CONTROL
MODERATE
SEVERE
1 mo
8 mo
21 mo
TIME AFTER DISTURBANCE
PCA Axis #2
PCA Axis #1
A
B
C
D
E
F
G
H
I
Diversity treatments
H: +F+R+M
M1: -F+R+M
M2: +F+R-M
L1: +F-R-M
L2: -F+R-M
Reference plots

Figure 3.12

Community states

To examine in greater detail the trajectories that experimental plots took in response to the disturbance and the release of the diversity press, I created transition diagrams to illustrate the dominant community "progression." Each subplot from the four data sets (Reference, THERM-CONTROL, MODERATE, and SEVERE) was classified into one of the six community states as outlined in the methods. In these diagrams (Figures 3.13-3.15), the circles represent the community states that were present in a census and the thickness of lines connecting the states represents the proportion of all subplots within a treatment making that transition. Thus, the thick lines illustrate the predominant pattern within the treatment and the thinner lines represent the variation within that pattern.

Reference plots

The predominant state within the reference plots throughout the experiment was fucoid dominated (Figure 3.13). More than 75% of these subplots remained in the fucoid state. Other states were also common, in particular, areas dominated by foliose red species. Although less abundant in overall area, foliose red-dominated states were also persistent throughout the experiment in those reference plots. Other states that occurred were transient: Cladophora-dominated, Balanus/Endocladia dominated, and barnacle-dominated states might persist for up to a year but would then change to other states,

often to the fucoid-dominated state. Although bare rock occurred and was created in these plots, it was not spatially extensive enough in any subplot in the censuses shown to force that sample unit to the bare rock-dominated state. I use these reference plots as a benchmark to compare diversity treatments and disturbance-level treatments. Because the character of the states in Figure 3.13 represent a large number of non-manipulated areas, they present a picture of the dominant pattern as well as the variability within the "normal" state of the community.

Figure 3.13. State diagram for the reference plots. Figure illustrates a sample of 5 census periods during the experiment to demonstrate typical variation throughout the experiment of non-manipulated plots. Circles represent one of the six community states described in the methods section. Legend denotes the percent of experimental areas making the transition between states across time. Thick lines indicate the dominant transitions and states. States that do not occur during a census are not shown.

Figure 3.14. State diagram for THERM-CONTROL subplots, all diversity treatments. Arrow indicates the point in time that the diversity press was released. See Figure 3.13 for more details.

Figure 3.15. State diagram for MODERATE disturbance subplots, all diversity treatments. Arrow indicates the point in time that the diversity press was released and the thermal stress was applied. See Figure 3.13 for more details.

Figure 3.16. State diagram for SEVERE disturbance subplots, all diversity treatments. Arrow indicates the point in time that the diversity press was released and the thermal stress was applied. See Figure 3.13 for more details.

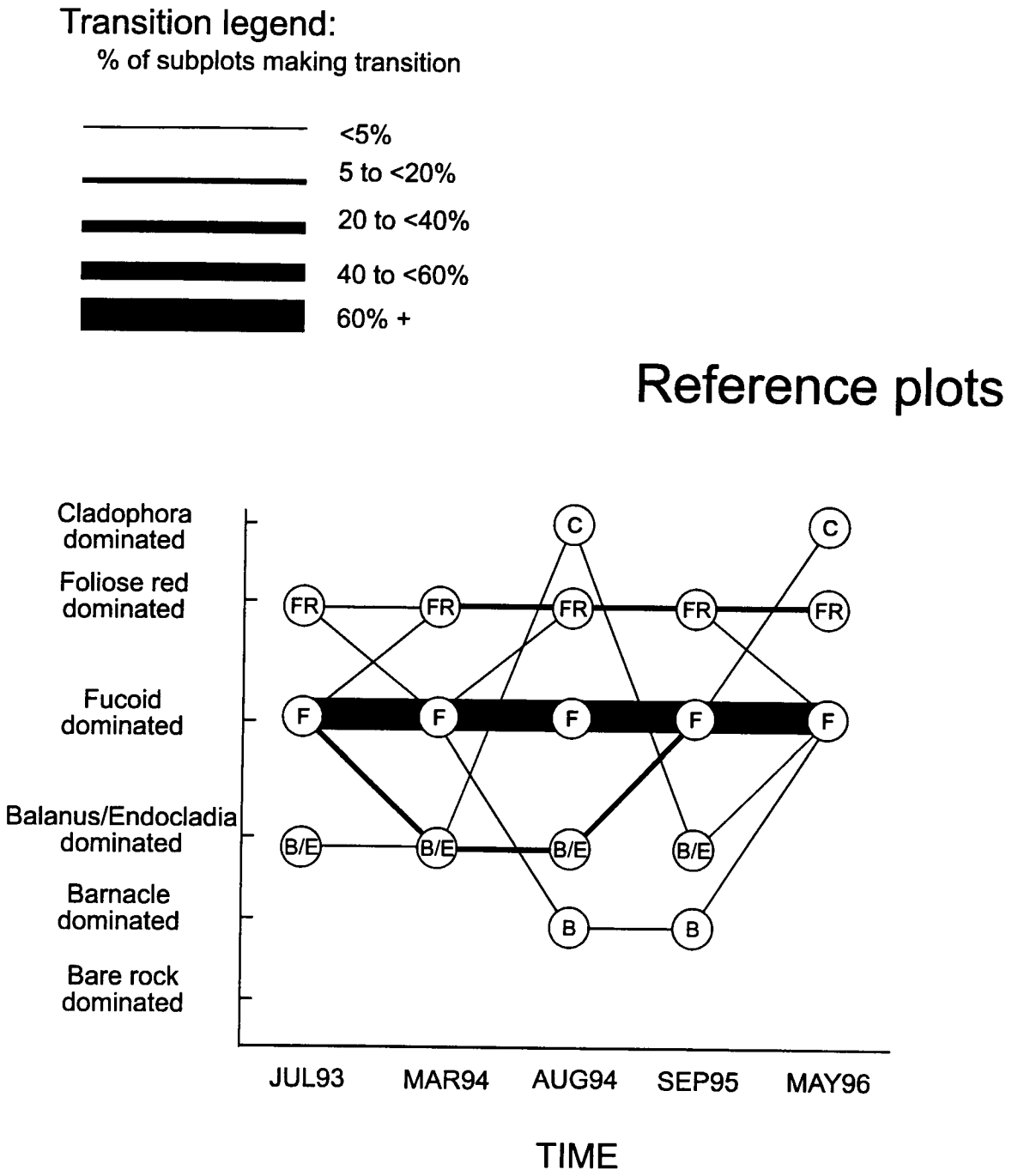
Transition legend:
% of subplots making transition
<5%
5 to <20%
20 to <40%
40 to <60%
60% +
Reference plots
Cladophora dominated
Foliose red dominated
Fucoid dominated
Balanus/Endocladia dominated
Barnacle dominated
Bare rock dominated
C
FR
F
B/E
B
JUL93
MAR94
AUG94
SEP95
MAY96
TIME

Figure 3.13

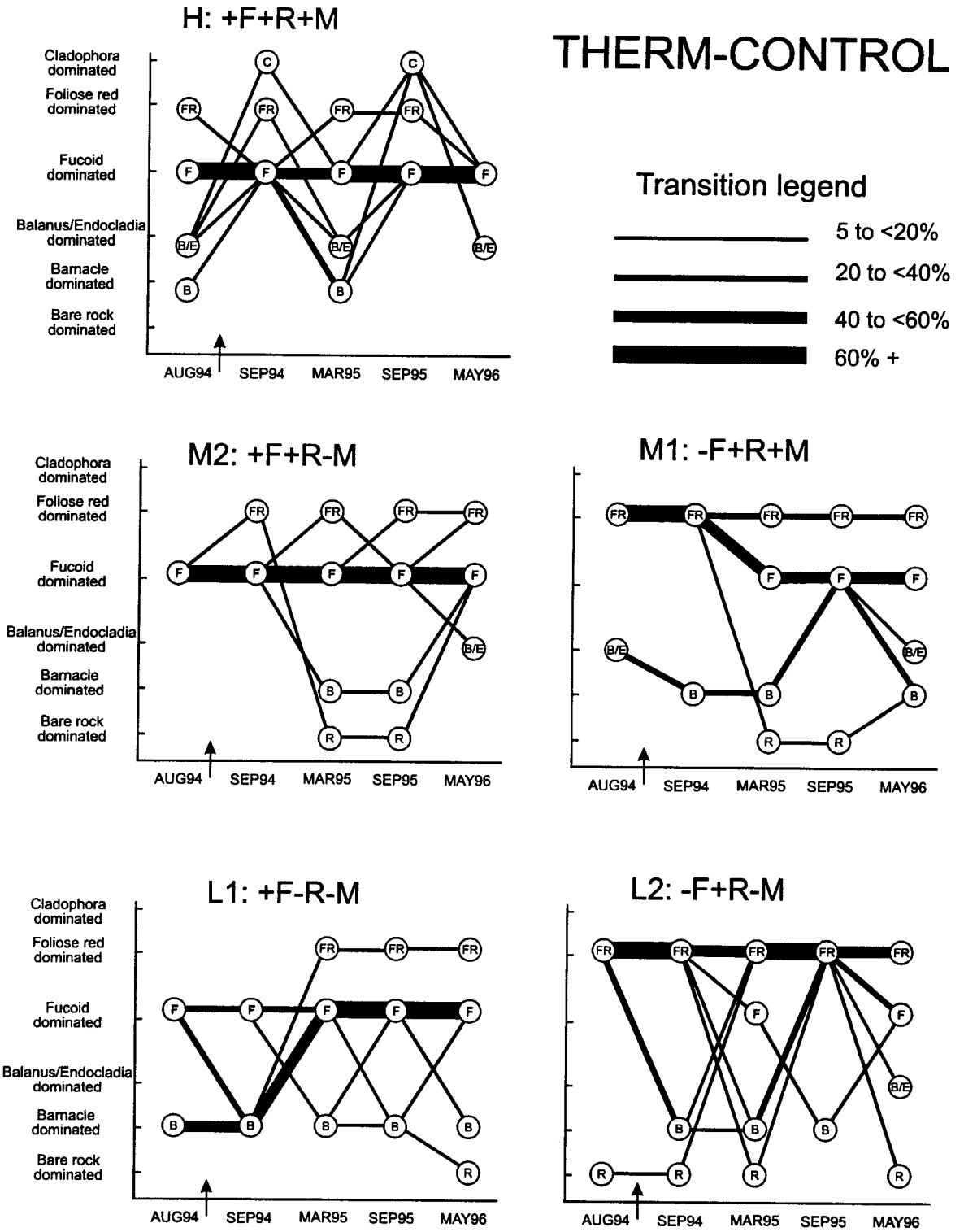
H: +F+R+M
THERM-CONTROL
Cladophora dominated
Foliose red dominated
Fucoid dominated
Balanus/Endocladia dominated
Barnacle dominated
Bare rock dominated
AUG94
SEP94
MAR95
SEP95
MAY96
Transition legend
5 to <20%
20 to <40%
40 to <60%
60% +
M2: +F+R-M
M1: -F+R+M
L1: +F-R-M
L2: -F+R-M

Figure 3.14

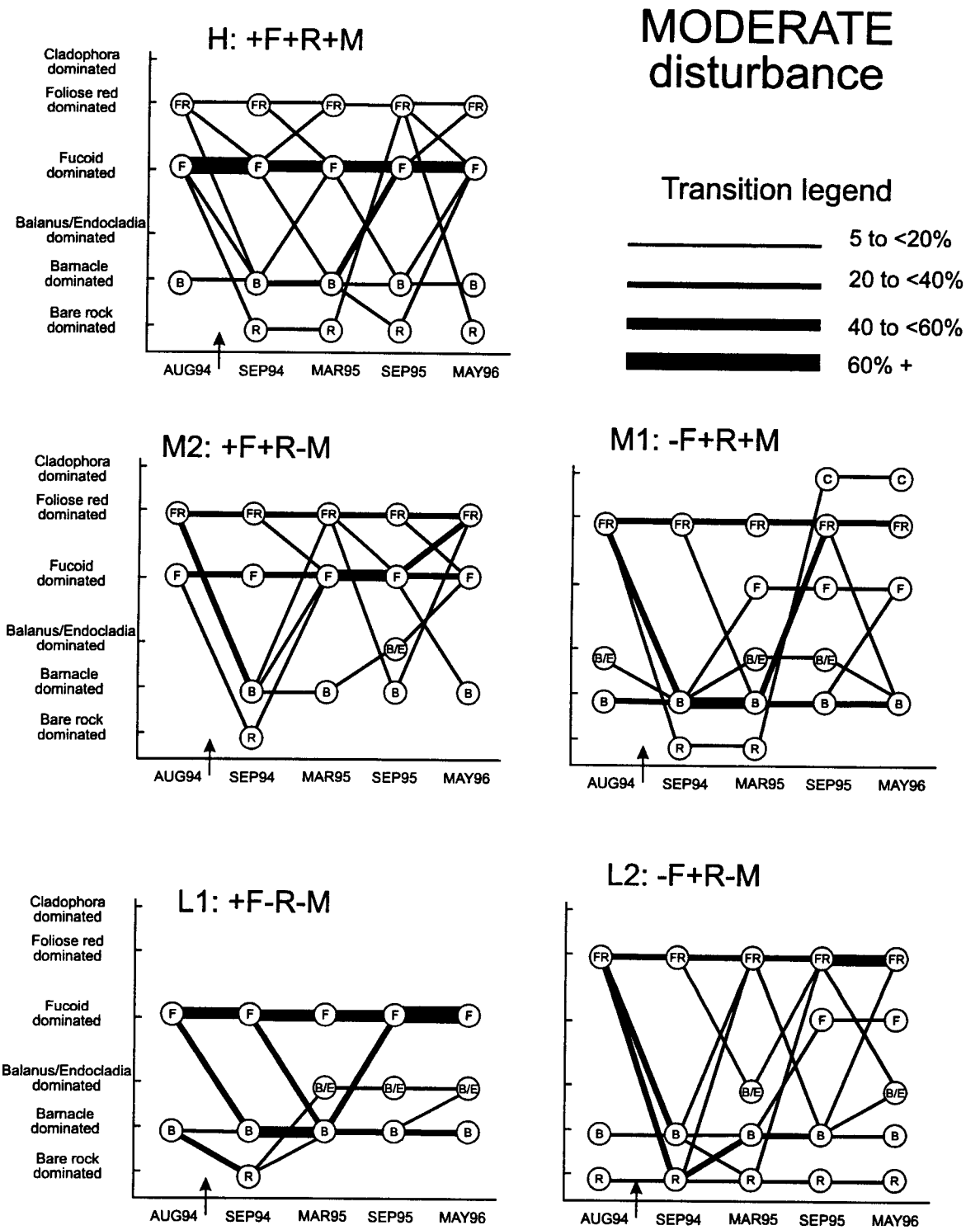
H: +F+R+M
MODERATE disturbance
Transition legend
5 to <20%
20 to <40%
40 to <60%
60% +
M2: +F+R-M
M1: -F+R+M
L1: +F-R-M
L2: -F+R-M
Cladophora dominated
Foliose red dominated
Fucoid dominated
Balanus/Endocladia dominated
Barnacle dominated
Bare rock dominated
AUG94
SEP94
MAR95
SEP95
MAY96

Figure 3.15

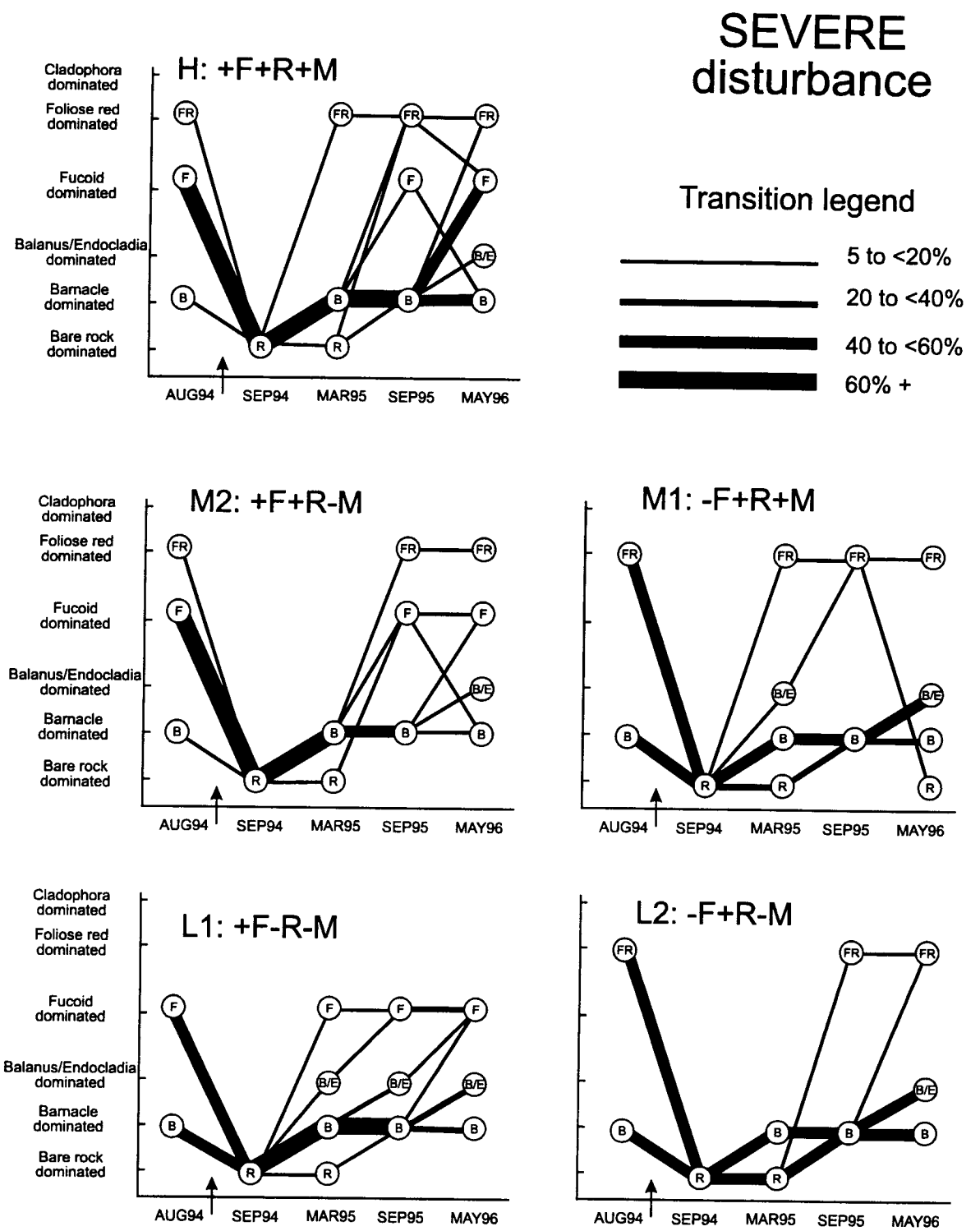
SEVERE disturbance
Transition legend
5 to <20%
20 to <40%
40 to <60%
60% +
H: +F+R+M
M2: +F+R-M
M1: -F+R+M
L1: +F-R-M
L2: -F+R-M
Cladophora dominated
Foliose red dominated
Fucoid dominated
Balanus/Endocladia dominated
Barnacle dominated
Bare rock dominated
AUG94
SEP94
MAR95
SEP95
MAY96

Figure 3.16

Recovery in stress-control plots

The thermal stress controls (THERM-CONTROL) were released from the diversity press in August 1994 and their progression after that point represents the "resilience" to a species deletion perturbation (*sensu* Pimm 1979, 1980). Two higher diversity control treatments (Figure 3.14; H, M2) were closest to the reference plots at the start of the resilience period (Figure 3.12A). For these treatments, the predominant state throughout the resilience period was fucoid-dominated, though other states were present but not persistent. Unlike the reference plots, the foliose red-dominated state was not persistent throughout this period in these two treatments. In the low diversity treatment (L1:+F-R-M) at the start of the resilience period, the barnacle-dominated state occupied as many subplots as the fucoid state (Figure 3.14). The diversity release in these plots led to a slow progression to states similar to the reference plots.

Stress-control plots that had fucoids removed during the diversity press also showed slow recovery to reference-like states (Figure 3.14; M1, L2). At the start of the resilience period, the mid diversity treatment (M1) was primarily in the foliose red-dominated state. Within 8 months, a majority of subplots had made the transition to the fucoid-dominated state and all of the subplots previously dominated by Balanus/Endocladia made the transition to the fucoid state by 14 months. Further, by the end of the monitored resilience period, the proportion of states in this treatment was roughly equivalent to the reference plots. However, the low diversity treatment (Figure 3.14; L2) showed little recovery to a primarily fucoid-dominated community. Although the states of L2 were similar to M1 at the start of the resilience period, the foliose red-

dominated state persisted throughout that period in the low diversity treatment. Thus, the persistence of stages that were typically not prevalent in the reference plots slowed the resilience of this low diversity treatment to reference-like composition.

Recovery in disturbed plots

The effect of the diversity treatments in MODERATE areas (Figure 3.15) was quite variable. The high diversity (H:+F+R+M) and mid-diversity (M2:+F+R-M) treatments were similar to the reference plots although in both treatments, a small proportion of subplots made transitions to bare rock-dominated or barnacle-dominated after the stress. Note that the proportion of foliose red-dominated states was high in M2 before the stress and remained prominent in this treatment. The low diversity treatment (L1:+F-R-M) also had some transition to different states (rock or barnacle only) but remained fucoid dominated. However, this treatment never developed any foliose red-dominated states. In the treatments that had excluded fucoids during the diversity press (M1, L2), there were also transitions to barnacle and rock states after the stress, but foliose red-dominated states remained prevalent throughout. However, fucoid-dominated states began to persist by September 1995, though at low abundance within the treatments. Note that these fucoid-dominated states arose from transitions from barnacle states but not from the foliose red-dominated states.

Within severely disturbed areas, the thermal stress reset all states to bare rock-dominated (Figure 3.16). The primary community trajectory for all treatments in these strongly effected areas was a progression from bare rock through barnacle stages and

eventually to algal dominated states. By the end of the monitored resilience period, the treatments originally most similar to the reference plots (Figure 3.16; H, M2) were again composed of reference-like states, though the abundance of the fucoid state was not dominant. The low diversity, fucoid-only treatment (L1, Figure 3.16), was similar although there were no foliose red-dominated states. The two treatments from which fucoids had been excluded during the diversity press (M1, L2) showed recovery patterns similar to the +fucoid treatments in the SEVERE areas in early stages with the exception that the fucoid state never appeared during the monitored resilience period (Figure 3.16).

Thus, the level of stress and diversity treatment interacted to produce different recovery patterns. The transition to reference states in the low diversity treatments (L1, L2) were clearly longer than in the higher diversity treatments either because of the persistence of non-prevalent states (L2; FR prevalent) or the lack of return of some common states (L1; FR absent) and this occurred at all disturbance levels. The higher diversity treatments with fucoids (H, M2) and that were very similar to reference plots at the start of the resilience period (THERM-CONTROL), recovered to such states quickly (MODERATE) or only slowly returned to such states (SEVERE). The mid diversity, fucoid-exclusion treatment (M1) was initially very different from the reference plots but with no stress, returned fairly quickly to the reference (Figure 3.14; M1). MODERATE disturbance slowed that recovery to fucoid states and the SEVERE disturbance prevented their return altogether within the monitored period.

Biomass recovery

Recovery to reference levels of standing biomass was strongly affected by level of disturbance (Figure 3.17; Table 3.7; DISTURB is significant for both MODERATE and SEVERE comparisons to controls). Although there appears to be a trend of a diversity treatment effect (Figure 3.17; e. g., compare treatments H and M1), such treatment effects were not statistically significant (Table 3.7).

Table 3.7. ANOVA of biomass recovery 21 months after thermal stress. Because of multiple comparison to controls, significance was adjusted by the Dunn-Sidák criteria (α= 0.05 at $p < 0.0253$) and boldface type indicates a significant effect. The dependent variable was $\ln[\text{biomass}_{\text{month21}}/\text{biomass}_{\text{reference average}}]$.

	MODERATE				SEVERE			
Source	df	MS	F	P	df	MS	F	P
TRT	4	0.248	2.03	0.1109	4	0.410	1.16	0.3479
DISTURB	1	0.798	6.54	**0.0149**	1	6.05	17.11	**0.0002**
TRTxDISTURB	4	0.015	0.12	0.9734	4	0.110	0.30	0.8741
BLK	4	0.288	2.36	0.0716	4	0.743	2.10	0.1043
ERROR	36	0.129			32	0.353		

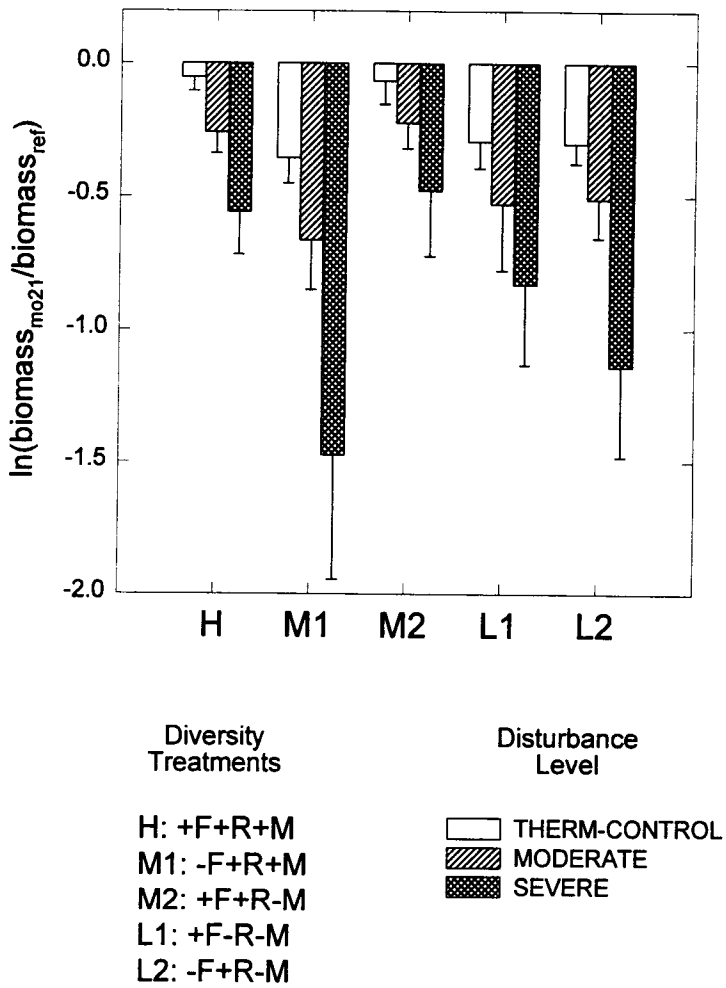

Figure 3.17. Standing (wet) algal biomass recovery by 21 months after thermal stress and the release of the diversity press. Proportional recovery calculated as ln[biomass$_{month21}$/biomass$_{reference\ average}$]. Error bars are standard errors, n=5. Values greater than zero would indicate full recovery to the reference.

DISCUSSION

Among the numerous factors that have been proposed to influence community stability (e. g., productivity: Stone et al. 1996; disturbance regime: Paine and Levin 1981; scale effects: Steele 1985, Rahel 1990), diversity has perhaps been the most contentious. This experiment highlights that diversity's influence on community dynamics is not simple and will depend on the characteristics of the stress as well as the characteristics of the species present in the community. Furthermore, factors such as the local regeneration pool, the life-history characteristics of dominant species, and the persistence of non-prevalent states will modify how a diversity effect will be manifested.

Resistance

This experiment demonstrated a few ways in which differences in diversity can modify the proximate effect of a strong perturbation. Because there were differences among diversity treatments in the abundance of many species as well as the community measures of biomass and cover, and the perturbation directly affected that abundance, the higher diversity treatments and especially those with fucoids, lost more from the thermal stress. Thus, in cases where higher diversity areas are more productive (Naeem et al. 1994, Tilman et al. 1996), they will have more to lose from a given stress. These results are similar to those at Cedar Creek, Minnesota (Tilman 1987, Tilman and Downing 1994) in which plots with the highest biomass lost the most during a extensive drought.

However, in that experiment, high biomass treatments were the low diversity treatments and thus low diversity treatments were the most severely affected.

For many species measures in this experiment, the great majority of the variation in "resistance" was attributable to the initial abundance of the species; diversity had little effect on the proportional change. This lack of a proportional diversity effect is probably attributable to the non-selective nature of the perturbation. Presumably, effects attributable to diversity will be caused by some difference or variation among species. For instance, if diversity has an effect on resistance to a stress, that effect may be due to differences in: how strongly the species are affected by the stress, how species protect themselves from a stress, or even how the species change the disturbance regime (Chapin et al. 1995, Denslow 1996). In Tilman and Downing's study (1994), because there were some species in the higher diversity treatments that were less susceptible to the drought than most species, the high diversity treatments experienced less proportional loss than low diversity treatments. However, if a stress affects all species in similar ways, we might expect diversity to have little influence. The morphology of the algal species manipulated in this community varied widely from thick leathery thalli (fucoids), to turfy species with dense clusters of blades (Mazzaella), to larger foliose plants (Mastocarpus), to bushy thalli (Endocladia), to dense spongy mats (Cladophora). However, apparently for most species measures, the intensity of this thermal stress overwhelmed these differences such that no species was proportionately less affected. The selectivity of a stress will depend at least on the magnitude and type of disturbing force and the characteristics of the species affected (Sousa 1985), with greater forces more likely to overwhelm species characteristics. Thus, it is expected that one class of stresses that are

likely to be non-selective are catastrophic perturbations and that diversity will have little influence in such disturbances.

The one apparent proportional diversity effect for resistance was the association of point diversity, or the average number of species/grid point, with the amelioration of the stress on canopy cover. Plots with several algal species at any given point have a much higher degree of structural complexity than plots with low point diversity. Structural complexity has been suggested as important in other studies of diversity both in the resistance to stresses (Frank and McNaughton 1991) and in the efficient use of resources (Naeem et al. 1995). Thus, this result suggests that overall canopy cover may be more resistant to loss if there are a variety of species to absorb the stress.

Resilience

The design of this experiment allowed me to evaluate community resilience to two types of deviation from the reference state: an environmental disturbance and a species deletion perturbation. Deviation from the reference by disturbance were of 3 categories: severe, moderate and no disturbance. Deviation from the reference by deletion of species ranged from no deletion (H), to the removal of one group of species (M1, M2), to the removal of all but a few algal species (L1, L2). Thus these low diversity treatments are the largest species deviations from the reference in this experiment. While both disturbance and species deletion deviations influenced resilience, there were also interactions between the two effects.

Recovery from large deviations caused by the species perturbations (Figure 3.14; L1, L2) were clearly dependent on which species were present. When only the fucoids were present at the start of recovery (L1), the collection of plots returned to states similar to the reference in less than a year. However, when Mastocarpus and Mazzaella were the only starting species, fucoid dominated states did not return throughout the resilience period. In contrast, recovery from large deviations caused by the thermal stress (Figure 3.16) produced similar recovery pathways among diversity treatments: rock-dominated, followed by barnacle-dominated, followed by some algal dominance. The initial diversity modified this in that the -fucoid treatments did not develop any fucoids in the 21 month resilience period. Thus, although the general successional pathways were similar, later states diverged.

Two reasons for the slow recovery in the two low diversity treatments were evident: 1) persistence of a non-reference state and 2) lack of a dominant group. First, in the low diversity treatment L1, it was the initial absence of the species that made up that persistent state (FR) that made full recovery to reference states slower. Throughout the monitored period (almost two years), the foliose-red state never appeared in the stressed plots. The two species that are the main components of this state, Mastocarpus and Mazzaella, have life history characteristics that do not facilitate rapid colonization. Mazzaella propagates primarily through vegetative growth. Although Mazzaella is resilient to damage to blades, removal of or damage to the crust severely retards its ability to recover (Olson 1985). Similarly Mastocarpus has a thick crust stage ("Petrocelis") that is remarkably resilient to many stresses (Dethier 1987), although the blades are less so. Apparently the persistent removal of species from treatment L1 during the diversity press

combined with the thermal stress which may have damaged any remaining crusts, removed even the most resistant stages of the species. Indeed, the only subplot in this diversity treatment to reach a foliose-red state (Figure 3.14; L1) was a subplot that, before diversity press, was dominated by Mastocarpus and throughout the press had a sizable cover of the basal crust stage. (As mentioned in Chapter 2, I did not attempt to remove all crust stages during the diversity press.) In the treatments in which fucoids had been excluded (M1 and L2), the foliose red (FR) state was quite persistent as the dominant state. This was particularly true for the lower diversity treatment. As explored in Chapter 2, this persistence in the low diversity treatment (L2 compared to M1), may be attributable to the facilitation of fucoid recruitment by low abundance species.

There was also a clear effect of the local "regeneration pool" (*sensu* Denslow 1996) on resilience and recolonization of algal species into these plots. If a species had been excluded from a plot during the diversity press, it returned much more slowly to even the severely disturbed areas than to plots in which a species had not been excluded (note the absence of fucoid states in M1 and L2 and the absence of the foliose-red state in L1, Figures 3.15 and 3.16). This result suggests a very local dependence for recovery (e. g., Type I, Sousa 1985). These experimental plots were slightly larger than one meter on a side and, for most species, propagule sources were within a few meters. However, the dependence of recovery on the presence of the species within the experimental plot suggests either a dependence on very close propagule sources or some facilitation of recruitment. Sousa (1984a) found similar dynamics for algal succession in patches made in mussel beds and other research (Farrell 1989, Kim and DeWreede 1996) in communities similar to this experiment have suggested similar, highly local recruitment

dynamics. These results imply that even local diversity reductions produce the dynamics that will be dependent on which species are present.

Thus, in this experiment, because high diversity treatments had higher overall abundance before the stress, they suffered the most loss. However, there was little indication of a proportional difference among diversity treatments or among dominant species. The non-selective nature of this thermal stress suggested an important distinction for predicting whether diversity will influence community dynamics. However, recovery from the stress was clearly influenced by initial diversity of the plots as well as the intensity of the disturbance. Areas severely disturbed followed similar recovery patterns regardless of initial diversity, although differences emerged by the end of the experiment. In contrast, in areas less disturbed, higher diversity treatments, especially those more similar to the reference states, recovered quickly, but low diversity treatments recovered slowly either because of some persistent non-typical states (foliose-red dominated), or the slow recovery of some typically abundant species (fucoid dominated). Thus, these results indicate that the effects of the reduction of diversity on resistance and resilience will be strongly contingent on the characteristics of the stress and the characteristics of the removed species.

CHAPTER 4

Experimental Manipulations of Biodiversity and the Consequences of "Aliasing"

ABSTRACT

One goal of recent biodiversity studies is to understand the ecological consequences of loss of diversity. Within that research, experimental manipulations of diversity promise to uncover causal relationships between diversity and selected responses. One necessary objective of this research is to determine which "component" of biodiversity (such as number of species, functional-group diversity or the uniqueness of species) contributes most to a response because the implications to conservation differ among components. However, intrinsic complexity of the manipulated variable (biodiversity) can confound studies attempting to explore causation. One condition is of particular concern because it is likely to be widespread: the misidentification of one biodiversity component as a different component, or "aliasing." Here I report a simulation model that investigates the ability of different experimental designs to detect broad biodiversity effects as well as to separate biodiversity components. These results show that alternative experimental designs will yield very different results under identical conditions. As such, care must be exercised when selecting an experimental design, interpreting and generalizing results, and comparing results among experiments.

INTRODUCTION

The consequence of the loss of biodiversity on ecosystem functioning and community stability is a major ecological concern and has spurred a great deal of new research (Solbrig 1991, Schulze and Mooney 1993a, Ehrlich 1995, Lamont 1995, Mooney et al. 1996). The motivations for this research are clear. Understanding how changes in biodiversity will affect ecosystem and community properties should allow us to better predict under what conditions this loss will be especially detrimental (both to the ecological systems and to humans) and should help us focus our conservation efforts (Lubchenco et al. 1991, Risser 1995, United Nations Environment Programme 1995).

Research directed at this issue has included assessments of biodiversity patterns (see Cowling and Samways 1995, Ricklefs 1995, Sepkoski 1995 for reviews), cataloging of functioning and services of ecosystems (Ehrlich and Mooney 1983, Ehrlich 1995, Mooney et al. 1995b), and attempts to correlate the two (Schulze and Mooney 1993a, Mooney et al. 1996, Silver et al. 1996). Although there have been attempts to establish this link through observational studies (e. g., Hurd et al. 1971, Frank and McNaughton 1991, Rodriguez and Gómez-Sal 1994, Silver et al. 1996), direct causal relationships cannot be inferred from observation. Thus, the most convincing demonstration of the relationship between biodiversity and ecosystem functioning and community dynamics is through experimental manipulation of biodiversity. Indeed, the high-profile nature of a few recent biodiversity experiments (Kareiva 1994, 1996, Naeem et al. 1994, Tilman and Downing 1994, Tilman et al. 1996) attests to the rarity of well-designed experiments and the perceived critical role of experiments in exploring hypothesized relationships.

One objective of this research has been to establish whether and under what conditions there are causal links between biodiversity and both ecosystem functioning and community stability. An important motivation behind this objective is that, although some relationships have been suggested for decades (Odum 1953b, MacArthur 1955, Elton 1958, Hutchinson 1959, Egerton 1973), hypothesized relationships have been challenged for a number of reasons. For example, community stability (a common response variable) is not necessarily a mathematical consequence of diversity (May 1971, 1972, 1973); typical measures of diversity may have little biological relevance (Hurlbert 1971); species diversity may be only noise within the more fundamental functional relationships (Walker 1992, Lawton and Brown 1993, Hay 1994); and strong effects may be due to single species (Paine 1969, Chapin et al. 1995, Power et al. 1996). Further, few experimental studies have been performed to directly test diversity's causative relationship to other ecological properties (McNaughton 1977) until recently. When some of these challenges were originally raised about the relationship between diversity and stability or diversity and ecosystem functioning, diversity was defined in the narrow sense as only the number and evenness of species. Even then, a wide-array of opinion existed on the expected relationship (Watt 1964, May 1973, Goodman 1975, Murdoch 1975, McNaughton 1977, Leps et al. 1982, Pimm 1984). It is still widely expected that extensive empirical investigations are necessary to resolve much of the dispute (Leps et al. 1982, McNaughton 1993, Kareiva 1994, 1996, Johnson et al. 1996).

A second objective of this research is to characterize the nature of the relationship for predictive purposes. As outlined by Chapin et al. (1995), predicting effects of loss of

biodiversity requires that we know several aspects of the species pool: 1) the number of species, 2) their relative abundance, 3) species uniqueness, 4) the impact of a species on a process and 5) the indirect effects of a species. Two important questions within this objective are: which components of biodiversity are most responsible for the causal link and where is the relationship the strongest? Answers to these questions should increase our ability to forecast consequences to expect when biodiversity is altered.

The number of potential relationships between biodiversity and ecosystem functioning and community stability is overwhelming (Risser 1995). Only by identifying where these relationships are strong and likely to be modified by human impacts, will we be able to effectively focus our conservation efforts (Walker 1992, 1995, Lamont 1995, Risser 1995). Thus, for both objectives, comparing results among systems and across different conditions within a system is critical.

However, manipulations of biodiversity face several logistical constraints. Manipulating diversity, for example, is often highly labor intensive, and thus sometimes impractical. Moreover, the potential low signal level of a diversity effect requires either a high degree of control over external factors (Naeem et al. 1994) or a large number of replicates (Tilman et al. 1996). These constraints will thus lead to less than optimum and/or very expensive designs. Furthermore, because the concept of biodiversity can include so many components and, therefore, multiple operational definitions are used, the field is open to considerable confusion about how to compare experimental results, what components of biodiversity are actually being tested, and how general the results are. One aspect of this dilemma is of particular concern. Because of the complexity of biodiversity and the correlation among biodiversity "components," there is the potential

to attribute the experimental effects to one component when in fact another component is responsible. This is not simply a semantic problem or a difference in biodiversity definitions, but a real challenge for experimental designs to pinpoint the actual cause of an effect. I call this misidentification of one biodiversity component as another "aliasing" and explain it in detail below.

In this chapter, I explore some of these limitations of biodiversity research. I used a simulation approach to answer how this complexity will influence our ability to achieve the objectives outlined above. In these simulations, I created different "species pools" with characteristics that emphasized different biodiversity components such as number of species, uniqueness of species, and diversity of functional groups. I then sampled these species pools with a variety of experimental designs similar to those used in published or in-progress experiments. The simulations were designed to answer the following questions. How well do different designs detect biodiversity effects? How well can they separate the effects of different biodiversity components? And how susceptible are these designs to detection of "aliased" factors? The results of the simulations clearly demonstrated that, even under identical conditions, different designs will yield different results and can potentially lead to false conclusions. Finally, I synthesize the general role diversity experiments can play most effectively, given their limitations and ambiguities, to increase our overall understanding of the ecological consequences of biodiversity loss.

COMPLEXITY OF BIODIVERSITY

Biodiversity components

There are numerous definitions of biodiversity and the utility of each is context dependent. This flexibility is often seen as an asset because it reflects assertions by biologists that many aspects of diversity are likely to be important but their importance will depend upon factors such as the composition of the species pool, degree of physical stress within the system, and even the scale of interest. Within the range of the scientific uses of the term, biodiversity has become an umbrella for a wide array of biological components, ranging from traditionally-defined diversity components (number and evenness of species) to structural diversity (Frank and McNaughton 1991, Naeem et al. 1994, Tilman 1994) to functional diversity (Noss 1990, Vitousek and Hooper 1993, Silver et al. 1996, Tilman 1996); from variety within a group of species to the variety of groups (Chapin et al. 1995, Denslow 1996, Ewel and Bigelow 1996), and from genetic diversity (Thorpe and Smartt 1995) to taxonomic diversity to landscape diversity (Schulze and Gerstberger 1993, Burke and Lauenroth 1995). These "biodiversity components" (Chapin et al. 1995) thus together comprise the biological variety at many scales. Although many authors have suggested how different kinds of variety may affect other aspects of ecological systems, three components of biodiversity in particular have received considerable attention, especially in empirical work: species uniqueness, functional diversity and species number. Undoubtedly, many other aspects such as structural diversity and genetic diversity will be important in many circumstances, but in

this paper I will use just these three to illustrate the complicated nature of biodiversity research and the need for clear distinctions.

Species uniqueness is the degree to which individual species in a system have properties that uniquely contribute to a given response (Chapin et al. 1995). This is also called species identity when a given effect is attributable specifically to one species; one needs to know the identity of the species that is lost from a system to predict the effects of the loss. The quintessential species identity effect is that of a keystone species (Paine 1969); removal of such a species will, by definition, have a large impact on a system (Bond 1993, Power et al. 1996). Extensive experimental effort has been devoted to investigating effects of strong species (e. g., Paine 1974, Menge 1976, Lubchenco 1978, Menge et al. 1994, Estes and Duggins 1995, Mittlebach et al. 1995, Hixon and Brostoff 1996, Navarrete and Menge 1996), but this work is not typically performed in the context of testing the effects of diversity. Although strong interactors have been documented in many systems, it is still not possible to predict a priori *which* species will be keystone species without some experimental characterization of a system (Menge et al. 1994, Power et al. 1996). Therefore, without knowledge of the relative importance of species within a system, the effects of loss of diversity in a system that is characterized by a single or a few strong interactors will be largely uncertain (Allison et al. 1996).

A second component of biodiversity is how the species pool is partitioned into functional groups (Körner 1993). Suggestions that "species are just noise" (Hay 1994) imply that the most appropriate level of resolution is at functional groupings (Walker 1992, 1995, Lawton and Brown 1993, Steneck and Dethier 1994, Ewel and Bigelow

1996, Silver et al. 1996). A wide variety of functional groups have been defined including trophic, structural, biogeochemical, and even the way species respond to specific disturbances (Körner 1993, Chapin et al. 1995, Silver et al. 1996) and it is expected that most species will be a member of several such groups (Chapin et al. 1995, Fownes 1995). Within the context of an experiment and a given response variable, species can be lumped into different, mutually exclusive groups to test for the importance of that grouping.

Two aspects of functional groups bear directly on questions of the effects of biodiversity. First, it may be the diversity of groups within a system that is important and as long as at least one species from each group is present, the number of species is not critical (Vitousek and Hooper 1993; type 3). This is a number-of-groups effect. An example of this could be the number of morphological types that create different kinds of spatial heterogeneity (Frank and McNaughton 1991, Naeem et al. 1994). The second aspect is the relative importance of different functional groups; although groups may have the same kind of effect on the response, the magnitude of the effect differs. For example, the relative contributions to productivity of different physiological groups of plants may be different (e. g., C4 plants vs. forbs in grasslands; Tilman 1996). This is not a number-of-group effect but a group-identity effect. Indeed, a keystone species can be considered a strong functional group that consists of a single species (Schulze and Mooney 1993b).

The third component of biodiversity that I will use in this paper is species richness or, simply, the number of all species in a given system. This is a common measure in

biodiversity studies (Hengeveld et al. 1995) and is called diversity *per se* in studies that attempt to separate simple number-of-species effects from other components of biodiversity (Vitousek and Hooper 1993). Chapin et al. (1995) suggest two principal reasons to expect that number of species will have important ecological consequences: 1) more species increase rates or efficiency of resource capture and 2) more species provide insurance from loss of ecosystem functioning due to large environmental changes.

Some components of biodiversity are likely to be highly correlated and, because of that, number of species may be a good a surrogate for biodiversity in general. That is, as the number of species decreases in a system, other components of biodiversity, such as the diversity within functional groups or structural diversity, will likely decrease as well. However, the relationship between biodiversity components is not always simple. For example, it is not clear if the prevalence of strongly-interacting unique species will *decrease* at higher diversity levels because speciose systems are likely to have more functional overlap (Lawton and Brown 1993, Wright 1996), or if the prevalence will *increase* at higher diversity simply because high diversity systems have a greater likelihood of including species with truly distinct characteristics (Fownes 1995). Furthermore, the correlation structure between biodiversity components is likely to vary considerably from system to system.

Shape

Another informative characteristic of the relationship between diversity and a response is its shape (e. g., linear, unimodal). Different shapes imply different

characteristics of the species pool (Vitousek and Hooper 1993, Tilman and Downing 1994, Tilman et al. 1996). Four possible relationships are illustrated (Figure 4.1A-D) for the simplest condition: the effect of number of species on the response with each species having equal contribution to the response. In the additive model (Figure 4.1A), each species contributes in a linear fashion to the response and removal of a given species has the same effect regardless of how many other species are in the system. In other words, there is no compensation. Although this may be an unrealistically simple relationship for many responses, it is convenient to use as a basic reference pattern when comparing experimental designs. More complex shapes will likely decrease the power of any given test unless specifically designed to detect that shape.

In the compensation model (Figure 4.1B), there is little change in response until many species are removed from a system. This is the expected relationship when species remaining in a system compensate for the removed species, perhaps because of competitive release or a favorable change in physical conditions. The conservation implications of such a relationship is that a system is relatively resistant to changes in a response as species are removed as long as several species remain. This has been hypothesized to be the most common pattern (Vitousek and Hooper 1993) and has been demonstrated in two experimental studies (Tilman and Downing 1994, Tilman et al. 1996).

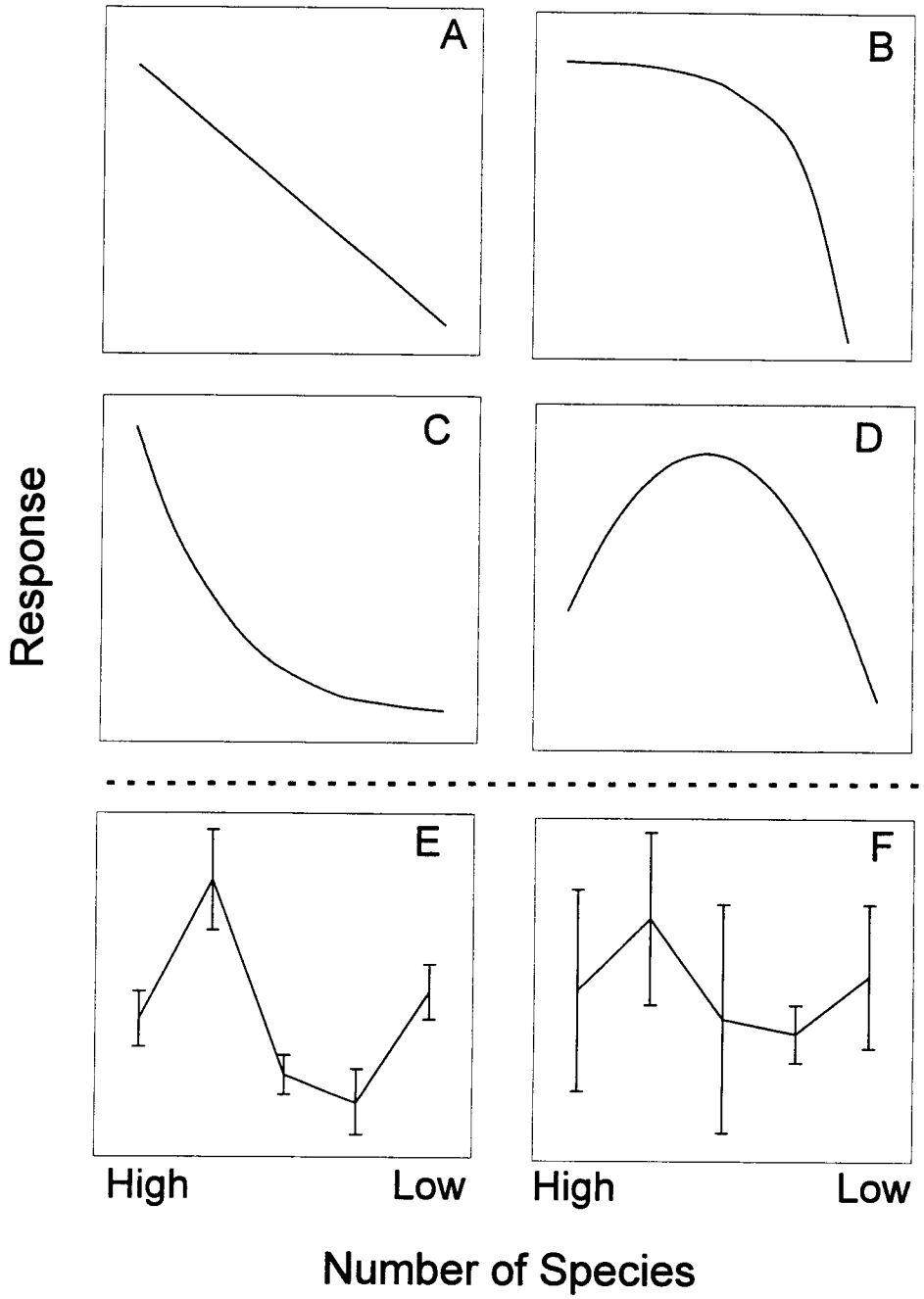

Figure 4.1. Illustration of potential shapes of the biodiversity/response relationship. A-D are hypothetical shapes that are expected under different species pool conditions: (A) simple additive, (B) compensation, (C) facilitation and (D) unimodal. E and F are examples of results with non-predictable shapes: (E) idiosyncratic and (F) no pattern.

Other shapes are possible, such as a facilitation model and a unimodal model. In the first (Figure 4.1C), full capacity of the response occurs only at high diversity and even a slight reduction in diversity drastically decreases the response. In the second relationship (Figure 4.1D), the highest values of the response occur at intermediate diversity. These relationships have received little attention in biodiversity literature and, although in some circumstances they may be the most appropriate models, I will not use them in the simulations.

Two other relationships deserve consideration here because their "shape" is of little use. In the idiosyncratic pattern (Naeem et al. 1995) (Figure 4.1E), the responses among different levels of diversity are significantly different, but not in a consistent manner. This may arise if the response variable is a complex function of many interacting variables. For example, if the response was the abundance of a focal species, and abundance of that species was dependent upon a number of strongly interacting species in the community, it would be expected that the response would vary inconsistently with number of species removed from the community, dependent more upon which species were removed and which remained. Therefore, although there is a demonstrated treatment effect from the statistical standpoint, there is little predictive information in the result about biodiversity. The other pattern is simply no effect of diversity treatments (Figure 4.1F). This may arise because there is no relationship between biodiversity and the response, because the relationship is weak in comparison to other effects whose variability masks the diversity effects, or because the design is inappropriate to detect the effect.

If we are to predict the consequences of species loss from a given system, it will be critical to separate the biodiversity components that are most responsible for effects and to determine the shape that best characterizes the diversity function. The conservation implications of an effect dominated by these different possibilities can differ in important ways. If the functions of an ecosystem are critically dependent upon a few species, it will be important to focus management efforts on those species (Walker 1992, 1995, Power et al. 1996). If a function is largely determined by number of species within a group or community, but the identity of those species is less important, then some fraction of species may be lost without substantial change in function (Menge et al. 1986, Ewel et al. 1991, Vitousek and Hooper 1993, Tilman and Downing 1994, Tilman et al. 1996). In such cases, conservation efforts that focus on particular species are probably less productive.

VARIETY OF EXPERIMENTAL DESIGNS

In the simulations described below, I explore three types of designs that are representative of experimental designs used in published or in-progress experiments and two hybrids of these design types. Table 4.1 details the specifics of the designs and some conventions used.

Table 4.1. Description of experimental designs used in simulations. The first part of each name distinguishes the class of design: "Group" = all groups are included in every treatment, "Fact" = manipulation by groups in a factorial manner, "Rand" = species selection within each replicate is random, and "Hybrid" = a combination of two of these types of designs. The "L" "M" or "H" at or near the end of each name distinguishes the relative number of sample units used in the design (L= low (20-21), M= moderate (80), and H= high (150-168)). Note that group affiliation is specifically considered in the Group and Fact designs, and ignored by the Rand designs. For all designs that use group identity as part of the design, it is assumed that the experimenter has correctly identified the species groupings that correspond to any real differences in the species pool. These groupings are arbitrarily set to three groups, each with the same number of species from the species pool. Note that some factorial designs contain treatments in which all species are excluded – these treatments are included for design balance and would be included in real experiments if there was a desire to test for **any** effect of the entire group of manipulated species.

Table 4.1

Design Name	Similar design used in:	Total number of sample units:	Experimental design description
GroupL	Naeem et al. 1994	21	Three treatments, seven replicates each. Three functional groups assumed and required in all treatments. Treatments differ by how many species represent each functional group. All replicates within a treatment have the same species. All species that are in the low diversity treatment are also in the mid diversity treatment. The high diversity treatment has the entire species pool. See Figure 4.2
FactL	Ch. 2 and Ch. 3 of this thesis	20	Partial factorial: Five treatments, four replicates each defined by the number and identity of the species groups present. There is one high diversity treatment, two moderate diversity treatments (Groups 1+2, Groups 2+3) and two low diversity treatments (Group 1, Group 2). When a group is included in a treatment, all species from that group are in each replicate.
FactM		80	Full factorial: Eight treatments, all combinations of the presence /absence of three species groupings. When a group is included in a treatment, all species from that group are in each replicate. See Figure 4.3.

Table 4.1 Continued

Design Name	Similar design used in:	Total number of sample units:	Experimental design description
RandL1		21	Seven treatments, defined by numbers of species (1, 2, 4, 6, 8, 12, and 24; three replicates each). Species used in each replicate are chosen by random draw from species pool. Any functional group differences within the species pool is ignored.
RandL2		21	Similar to RandL1 with three treatments (2, 8, 24 species; seven replicates each).
RandM		80	Similar to RandL1 with eight treatments (1, 2, 4, 6, 8, 12, 18, and 24 species; ten replicates each). See Figure 4.4.
RandH	Tilman et al. 1996	150	Similar to RandL1 with seven treatments: 1, 2, 4, 6, and 8 species with 20 replicates each, and 12 and 24 species with 25 replicates each).
HybridM		80	Eight treatments, roughly similar RandM (3, 6, 9, 12, 15, 18, 21, 25 species; ten replicates each). However, random species draws are made within each of the three species groupings, to guarantee representation of all groups in each treatment. See Figure 4.5.
HybridH		168	24 treatments, in three species-number levels; Within each species-number level, the treatments form a full-factorial design of the presence/absence of 3 species groups (similar to FactM); In the low species-number level, each functional group is represented by 1 species randomly chosen from the group's species pool; in the moderate level, four species; and in the high level, eight species. Each treatment has 7 replicates. See Figure 4.6.

In "Group" type designs, treatments are structured by how many species from each group are in each replicate with the constraint that all groups are represented in all replicates (Figure 4.2). A design similar to GroupL (but with less replication) was used by Naeem et al. (1994, 1995) in the Ecotron facility. In that experiment, the different "groups" were trophic levels (primary producers, primary consumers, secondary consumers, and decomposers). By forcing all groups to be present in every treatment, the researchers removed the substantial confounding effect of a missing trophic level in some of the treatments and could therefore more reliably attribute the effects seen to the numbers of species present. This design is, thus, appropriate to explore the effects of diversity *within* a given group structure.

In factorial type designs (Figure 4.3), the primary manipulated factor is which groups are present. Designs such as these directly address whether experimental effects are attributable to specific groups of species. While these designs do not directly manipulate species number, they do so indirectly: treatments with all groups present are high diversity treatments and treatments with only one group are low in diversity. What constitutes a valid species group will depend largely on the research question: grouping by species physiology (Tilman 1996), by species morphology, "life-form" and/or taxonomy (Steneck and Dethier 1994, Denslow 1996, Ewel and Bigelow 1996, Tilman 1996, Allison Chapters 2 and 3), or by consumer type (Menge et al. 1986, Huston and Gilbert 1996). Many other potentially informative groupings are possible. For example, in the experiment discussed in Chapters 2 and 3, I included a miscellaneous group of species united only by their low abundance.

Figure 4.2. Illustration of the experimental design, GroupL. The 24 species in the species pool are represented by letters of the alphabet and divided into three groups. Treatments are structured by the number of species from each group and there are only three treatments. All replicates within a treatment are identical. For lower diversity treatments, species selection from the group is random, although the species that are in the lowest diversity treatment must also be in the mid diversity treatment. See Table 4.1 for more specifics of this design.

Figure 4.3. Illustration of the experimental design, FactM. Treatments are structured by which groups are present and all combinations of groups presence or absence are used. All replicates within a treatment are identical and all species within a group are present if the group is present. Replicate structure for only 3 treatments is shown. See Table 4.1 for more specifics of this design.

Figure 4.4. Illustration of the experimental design, RandM. Treatments are structured by the number of species present in each replicate. Each replicate within a treatment is constructed by randomly selecting species from the pool, therefore replicates within a treatment are the same only by the number of species present. See Table 4.1 for more specifics of this design.

Figure 4.5. Illustration of the experimental design, HybridM. This design is a hybrid of Group- and Rand-type designs. It is similar to RandM (Figure 4.4) because each replicate is constructed by random selection from the species pool, with the added constraint that each group must be present in all replicates. See Table 4.1 for more specifics of this design.

Figure 4.6. Illustration of the experimental design, HybridH. This design is a hybrid of Fact- and Rand-type designs. The structure of the treatments is by two factors: which groups are present (in a factorial manner) and the number of species from each group that make up the replicate. It is similar to RandM (Figure 4.4) because the species for each replicate are chosen by random selection. See Table 4.1 for more specifics of this design.

GroupL

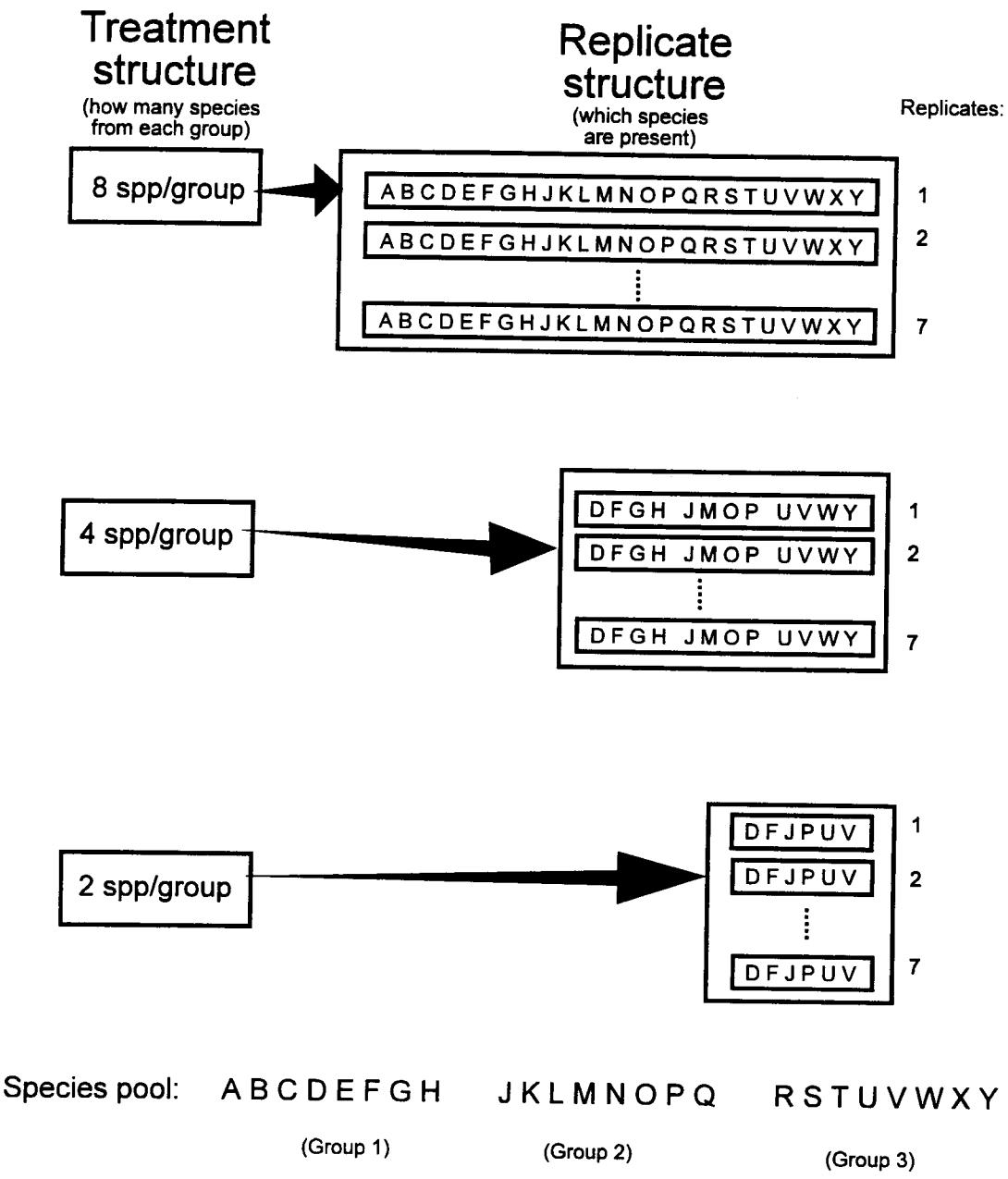

Figure 4.2

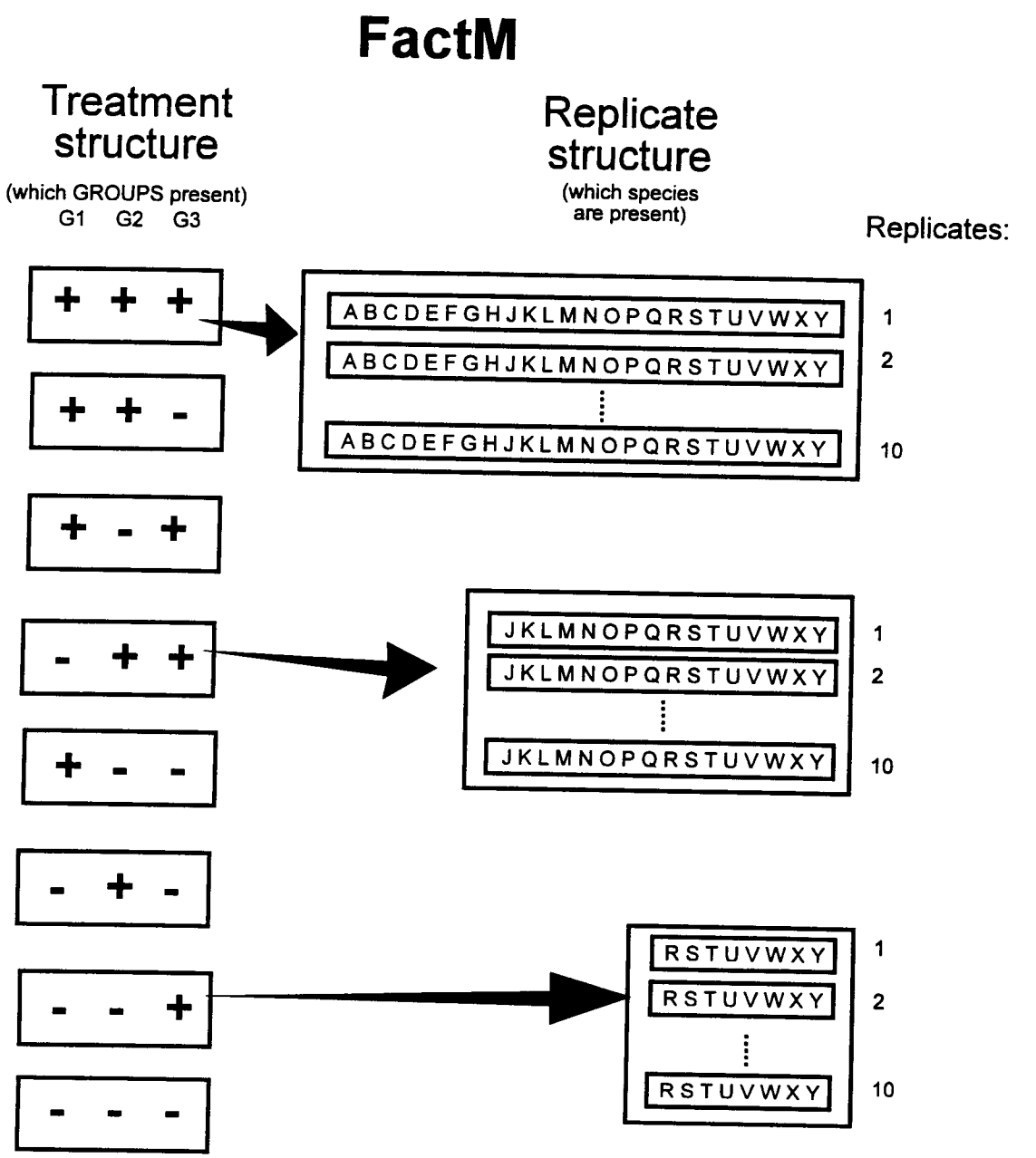
FactM
Treatment structure
(which GROUPS present)
G1 G2 G3
Replicate structure
(which species are present)
Replicates:
+ + +
+ + -
+ - +
- + +
+ - -
- + -
- - +
- - -
ABCDEFGHJKLMNOPQRSTUVWXY
ABCDEFGHJKLMNOPQRSTUVWXY
ABCDEFGHJKLMNOPQRSTUVWXY
1
2
10
JKLMNOPQRSTUVWXY
JKLMNOPQRSTUVWXY
JKLMNOPQRSTUVWXY
1
2
10
RSTUVWXY
RSTUVWXY
RSTUVWXY
1
2
10

Figure 4.3

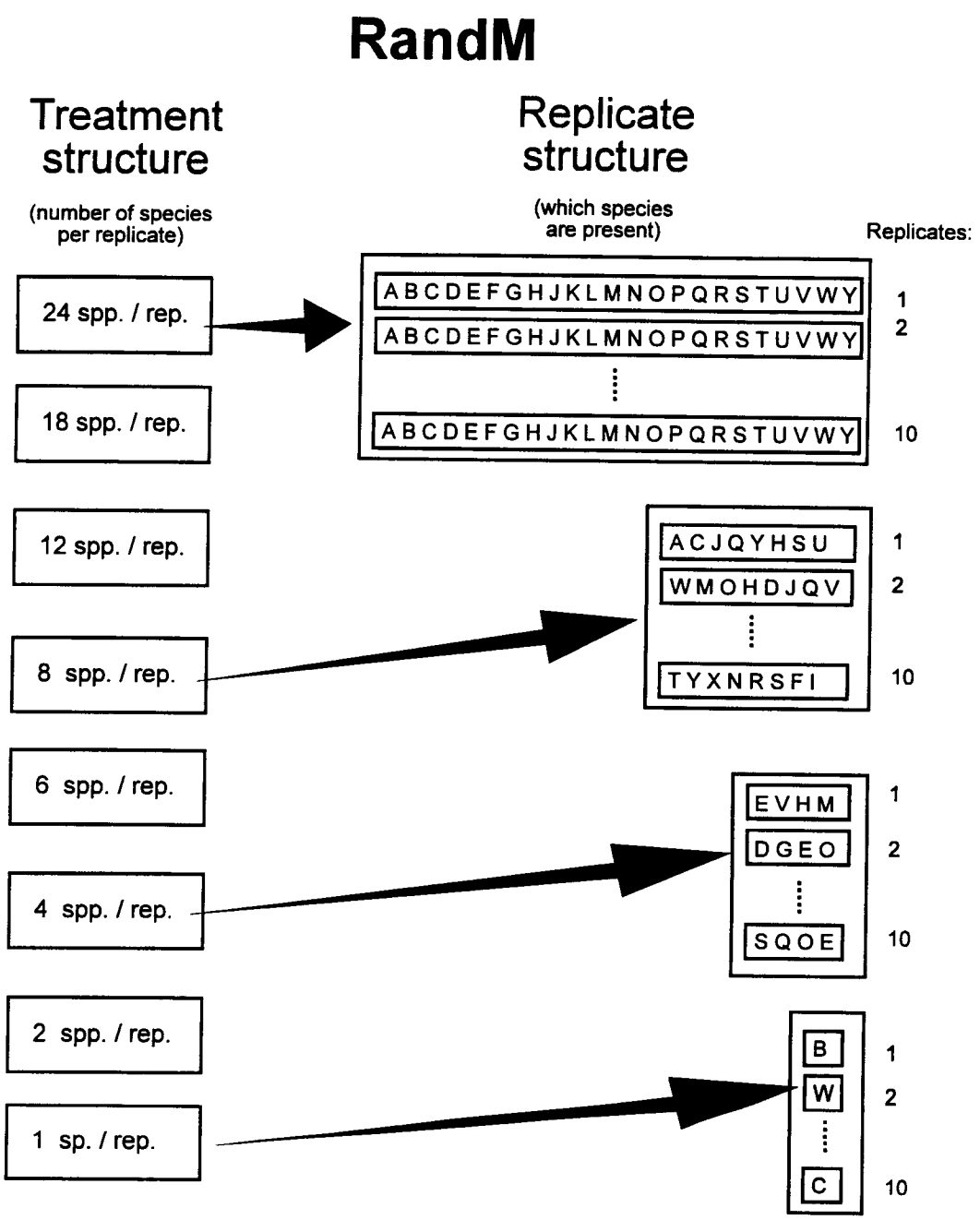
RandM
Treatment structure
(number of species per replicate)
Replicate structure
(which species are present)
Replicates:
24 spp. / rep.
18 spp. / rep.
12 spp. / rep.
8 spp. / rep.
6 spp. / rep.
4 spp. / rep.
2 spp. / rep.
1 sp. / rep.
ABCDEFGHJKLMNOPQRSTUVWY
ABCDEFGHJKLMNOPQRSTUVWY
ABCDEFGHJKLMNOPQRSTUVWY
1
2
10
ACJQYHSU
WMOHDJQV
TYXNRSFI
1
2
10
EVHM
DGEO
SQOE
1
2
10
B
W
C
1
2
10

Figure 4.4

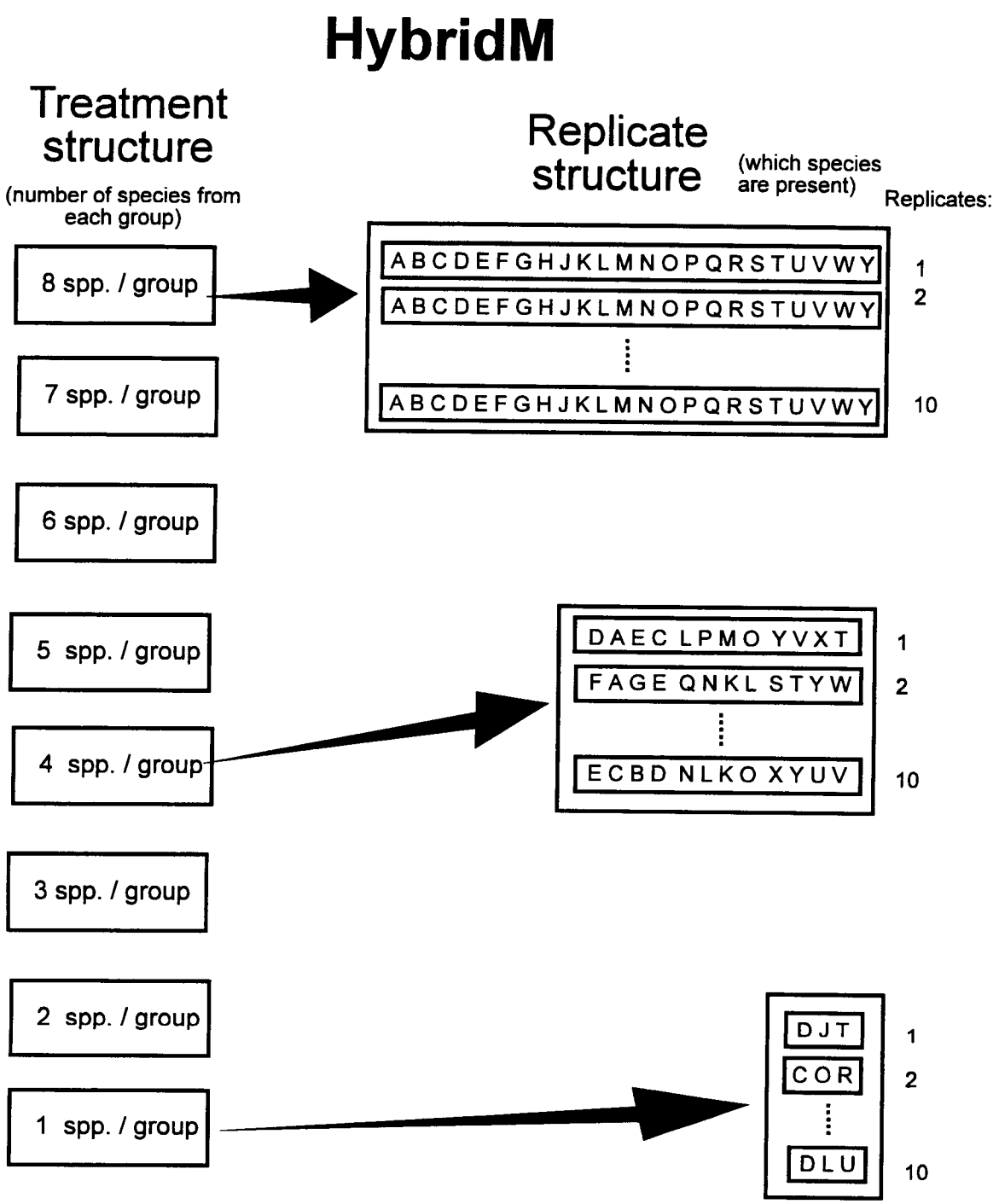
HybridM
Treatment structure
(number of species from each group)
Replicate structure
(which species are present)
Replicates:
8 spp. / group
7 spp. / group
6 spp. / group
5 spp. / group
4 spp. / group
3 spp. / group
2 spp. / group
1 spp. / group
A B C D E F G H J K L M N O P Q R S T U V W Y
A B C D E F G H J K L M N O P Q R S T U V W Y
A B C D E F G H J K L M N O P Q R S T U V W Y
1
2
10
D A E C L P M O Y V X T
F A G E Q N K L S T Y W
E C B D N L K O X Y U V
1
2
10
D J T
C O R
D L U
1
2
10

Figure 4.5

HybridH

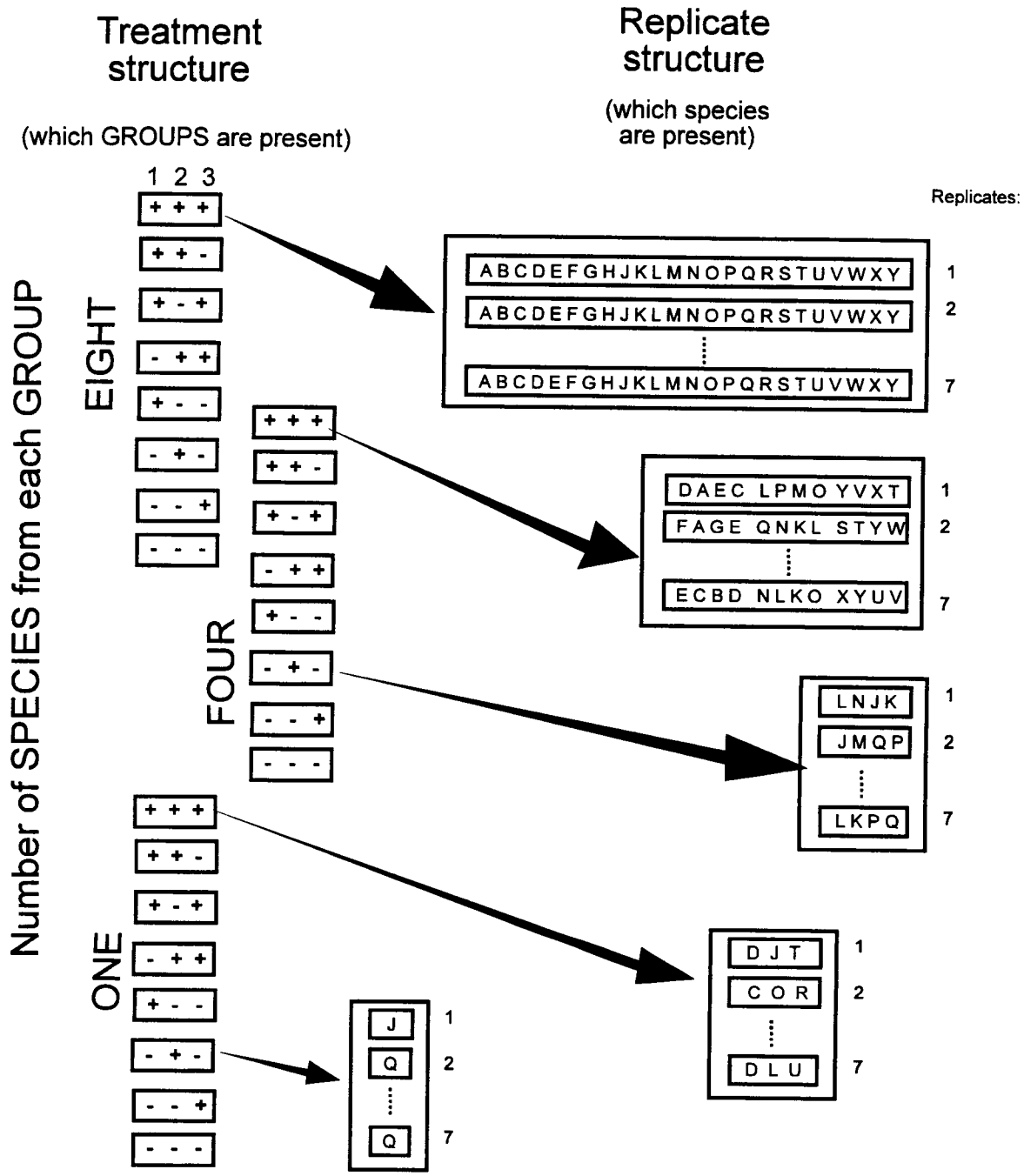

Figure 4.6

In designs represented by RandM (Figure 4.4), the primary manipulated factor is the number of species in each replicate, similar to "Group" type designs, but there is an important design twist. In an attempt to remove biases created by species identity, those species actually used for each replicate are determined by random selection from the species pool (Tilman et al. 1996). Using a design similar to RandH, Tilman and colleagues (1996) created a diversity gradient of 1 to 24 grassland plant species in experimental plots. They controlled for total abundance by ensuring that each plot was planted with the same total number of seeds even though number of species differed.

Besides testing these three types of designs in these simulations, I have included two hybrid designs. HybridM (Figure 4.5) is much like "Rand" designs in that each replicate is constructed through random selection from the species pool but has the added constraint (similar to GroupL) that all species groups are represented in every replicate. HybridH (Figure 4.6) combines a factorial design with the random selection process from "Rand" designs.

For the purposes of comparison, some key aspects of these designs separate them:

- **Composition of replicates:** In "Group" and "Fact" designs, all replicates within a treatment are identical; the same species are included in each. In contrast, for "Rand" designs, the actual species used for each replicate within a treatment are selected randomly from the entire species pool.
- **Principal factor manipulated:** In "Group" and "Rand" designs, treatments are defined by the number of species in the treatment. In "Fact" designs,

species are lumped into groups and treatments are defined by presence/absence of groups.

- **Use (or non-use) of group structure:** In the "Group" design, every treatment has representation of all functional groups. In "Fact" designs, treatments are an explicit manipulation of the presence/absence of the functional groups and all (or most) combinations of groups are included. In "Rand" designs, any group structure in the species pool is ignored in treatment construction, but because of the selection process, the experiment will likely include most or all combinations of groups.
- **Nesting of low diversity species sets into higher diversity sets:** For the "Group" design, the moderate diversity treatment includes all species used in the low diversity treatment plus others. Thus, for this design, one set of species is not manipulated. In "Rand" and "Fact" designs, because of their replicate or treatment construction, some moderate diversity treatments may not include species that are present in low diversity treatments.

SIMULATION METHODS

The flow of the simulation analysis is illustrated in Figure 4.7. First, a species pool was created with the desired rules of relationship among species and the response. For example, in a pool with characteristics illustrated in Figure 4.1A, each species would add equally to the response with no compensation. For a keystone effect, a similar pool would be created except that one species would have a strong effect on the response

relative to the other species in the pool. Table 4.2 lists all the species pools created for the simulations in this paper and quantitative details are provided in Appendix 1.

I then sampled from these pools by the rules of the experimental design under test (listed in Table 4.1). For example, for design RandH, I created 150 sample units, 20 of which had only one species, 20 sample units had 2 species, and so on. By the design constraints, species assigned to each sample unit were chosen randomly from the species pool. Each time the design was created, new random species assignments were made.

Then, a response was calculated by the rules of the relationship of the species pool and whatever species were assigned to the sample unit. The "response" here is equivalent to the "data" from an experiment. For example, for a species pool consisting of a simple additive relationship, a sample unit with ten species would have a response twice that of one with five species. In real diversity experiments, response variables have included productivity, nutrient retention and community response to a disturbance. Many guidelines for appropriate measures for such experiments have been suggested (Pimm 1984, Vitousek and Hooper 1993, Chapin et al. 1995, Lamont 1995, Risser 1995). The calculated response in these simulations is not intended to represent any particular measure. Instead, a generic response is simulated for which any univariate measure may be substituted. The characteristics of this response are explored with enough breadth to make it applicable to most real tests. Furthermore, in this study, a significant relationship between biodiversity and the response is detected by linear regression and therefore the direction of the relationship is also unimportant here; an inverse relationship is reported in the same manner as a direct relationship.

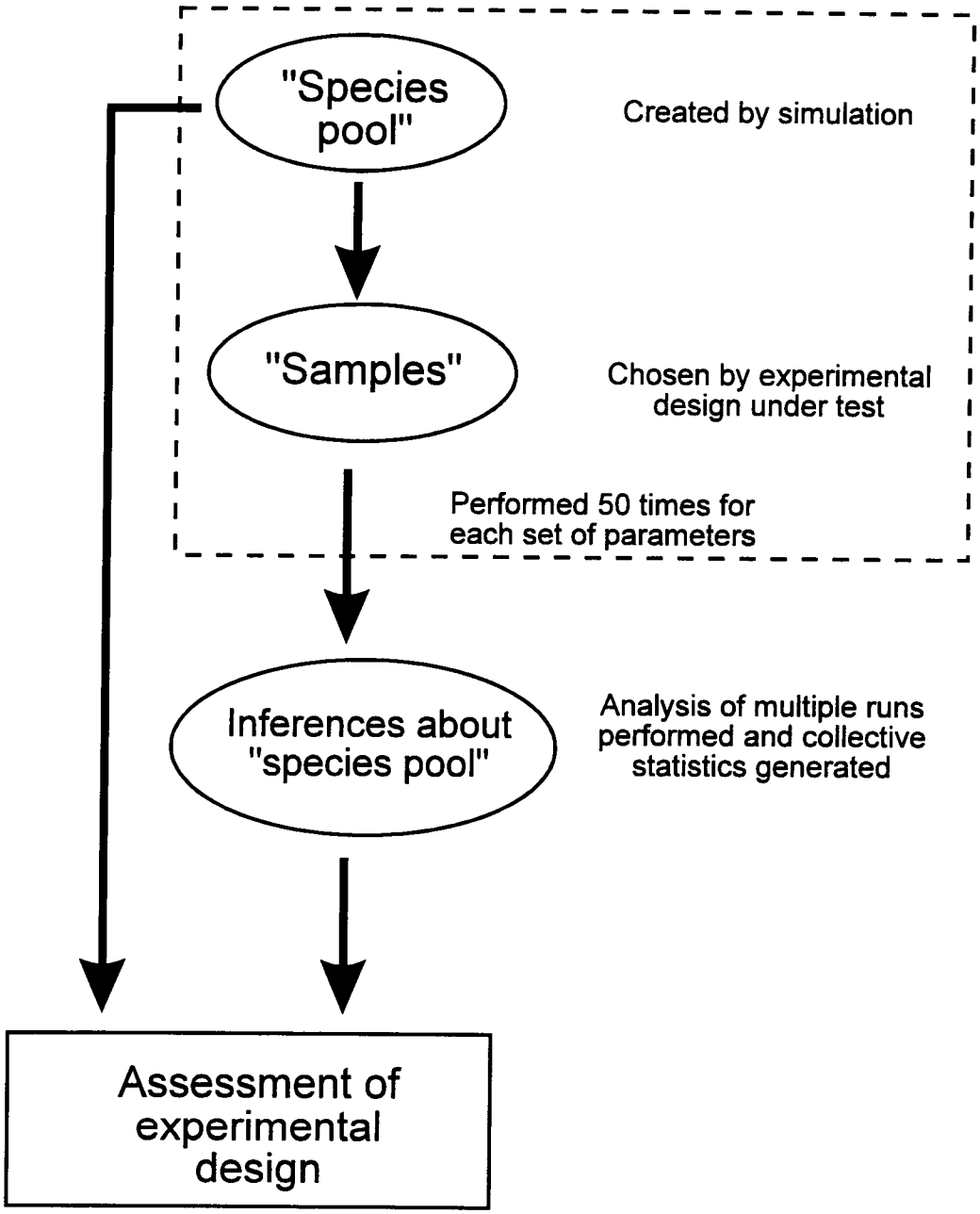

Figure 4.7. Simulation and analysis flow diagram showing the main components of the analysis of one experimental design. Multiple sets of 50 runs are performed throughout the range of S:N ratios in Series 1 simulations and the biodiversity component under test in Series 2 simulations.

Table 4.2. Description of the models of species pools used in the simulations. See Appendix 1 for the quantitative description of the models.

Model Name	Where model is used	Description
		Species Number effects
Simple additive number-of-species	Fig 4.9A Fig 4.10	The response is the sum of the effect of each species present. In this model, all species have the same effect on the response (Figure 4.1A).
Variable species spread	Fig 4.14	Similar to the Simple additive model, except that there is variability in the amount that each species contributes to the response. The deviation from an average amount is determined by the parameter "species spread." At high values of species spread, the effects of species will include negative and positive effects.
		Species Identity effects
Simple Keystone effect	Fig 4.9B Fig 4.11	The response is determined by the presence or absence of a single species in Group 1. All other species have no effect on the response.
Keystone + species number	Fig 4.16	The response is the sum of the effect of each species present. One species in Group 1, if present, has an effect on the response that is determined by the parameter "keystone strength." This parameter is scaled relative to the effect size of each other species.

Table 4.2 continued

Model Name	Where model is used	Description
		Group effects
Group diversity effect	Fig 4.9C	The response is the sum of the number of functional groups present in a treatment. Species within each group are perfectly redundant; group contribution to the response requires only one species of the group to be present.
Group difference	Fig 4.12	The response is the sum of the effect of each species present and is, thus, an additive species effect. However, the effect size for each species depends on group affiliation. Group 1 species have a relatively large effect, Group 2 species have a weak effect, and Group 3 species have no effect.
Variable group effect	Fig 4.15	Similar to Group Difference model, except the difference among the groups is determined by the parameter "group multiple factor" in the following manner: Group 1 effect = multiple factor Group 2 effect = multiple factor/2 Group 3 effect = 1 (constant throughout) Therefore, when the multiple factor is 10.0, species in Group 1 have ten times the effect on the response as species in Group 3.
		Other effects
Idiosyncratic	Fig 4.13	The response for a given treatment is random with respect to biodiversity components, but is equal for all replicates within the treatment; therefore there will likely be significant differences among treatments, but of an apparently random nature as in Fig 4.1E.

Because we can expect performance of a given experimental design to depend upon the strength of the "diversity signal," I controlled the experiment-wide signal-to-noise ratio ("S:N ratio"). This was done by first determining the range of responses across all sample units without noise, and then adding the appropriate amount of white noise to all sample units to yield the desired S:N ratio (Figure 4.8). For example, if the range of responses was equal to 1.0, and the desired S:N ratio was 2.0, a random number from a uniform distribution from -0.25 to +0.25 (range = 0.5; hence, a noise strength one-half of the signal strength) was added to each replicate value. Note that a *high* S:N ratio is equivalent to *low* variance. In these simulations, S:N ratio is equivalent to the strength of the experimental effect in a real system. The noise serves to represent the uncontrolled factors in an experiment that determine the detectability of the diversity effect.

One simulation run for a given design, species pool, and set of parameters produced a single "result" that was analogous to the result of a single real experiment. For most simulations, this process was repeated 50 times for each design at each set of parameters (Figure 4.7). Each of these repeats was analyzed with forward linear regression (see below) and the collective results of these repeats were summarized graphically. For the determination of the minimum S:N ratio for reliable detection (Series 2, below; Figures 4.14-4.16, left panels), the experimental design was tested at each given set of parameters across a large range of S:N ratios (using 50 runs at each S:N ratio).

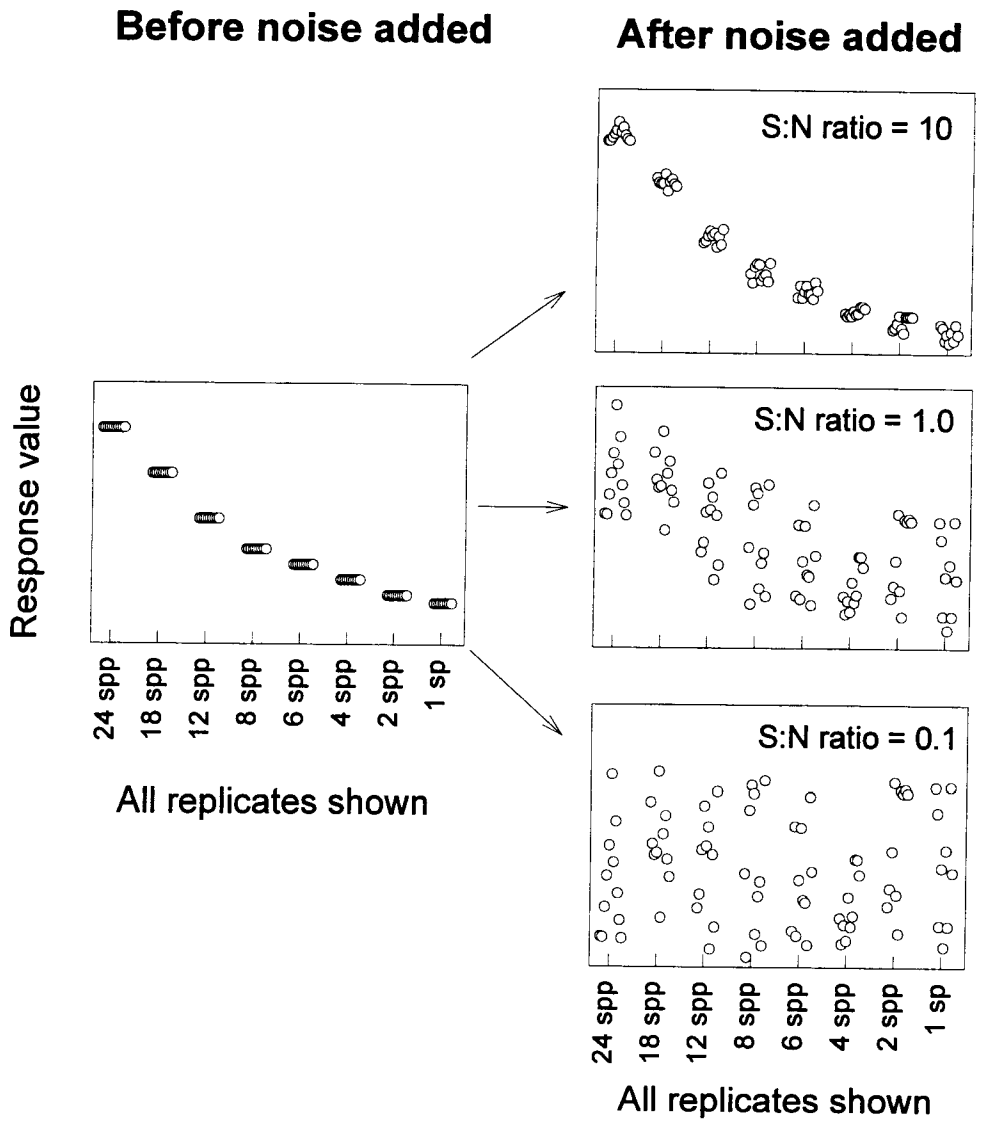

Figure 4.8. Illustration of signal to noise ratio (S:N ratio) and the consequence of adding different levels of noise to a signal. Experimental design used is RandM with a simple additive effect of species number. The panel on the left illustrates the effect with no noise and the three panels on the right illustrate three levels of noise added to the signal. All replicates within each diversity level are shown.

The simulation that controlled the creation of the species pools, the sampling by the experimental designs and the calculation of the responses were all performed by sets of Pascal programs. Statistical analyses of individual results and collections of results were performed by SAS for DOS (SAS Institute Inc. 1989) in batch mode.

LOW POWER AND "ALIASING"

In these tests of experimental designs, I was particularly interested in two conditions. The first was the non-detection of real biodiversity effects or the power of a design to detect a simulated effect. Given that the effect exists (as guaranteed here by the simulation), non-detection will occur for two reasons: other effects in the system overwhelm diversity effects (here simulated by low S:N ratio, that is, high unexplained variance) or the design chosen is inappropriate to detect the dominant biodiversity component. An example of the latter is the inability of a design to detect a keystone effect because the keystone species is included in all sample units (which could occur in design GroupL).

The second condition was the misidentification by the experimental design of one component of biodiversity as the primary cause, when in actuality, a different component was the primary determinant. I call this misidentification an "alias." The term "aliasing" is borrowed from signal analysis theory that uses the term to describe a condition where the frequency of a signal that is undersampled will be detected as a different frequency (de Coulon 1986, Candy 1988). The phenomenon in biodiversity studies is, thus,

analogous in that a natural pattern is not adequately sampled by an experimental design to determine the actual cause of the pattern of interest.

A simple example demonstrates the phenomenon. The experimental design RandH has several treatments, each with a different number of species. The particular species used in each sample unit is determined by a random draw from the species pool. This design was used with much success by Tilman and colleagues (1996) to demonstrate biodiversity effects on grassland productivity and nutrient use. When the species pool analyzed by this design has an additive relationship between the number of species and the response, the resulting sampling of the species pool shows the expected monotonic relationship (Figure 4.9A). However, if the response is determined by a single species in the species pool (e. g., a keystone species), the resulting sampling by this experimental design also appears to be an additive number-of-species effect (Figure 4.9B). This occurs because in high diversity treatments the keystone species is present in all replicates and therefore the calculated *average* response is large. When the treatment is composed of only one half of the species pool, the keystone is present, on average, in one half of the replicates and the calculated response for the treatment is one half of the high diversity treatment. Similarly, Figure 4.9C demonstrates the apparent relationship between number of species and the response when the response is not determined by the number of species *per se*, but instead by three groups of species (group diversity effect, Table 4.2). In this case, the apparent relationship after sampling is a compensation-type curve. In these latter two cases, the patterns detected by the experimental designs were "aliases" of a number-of-species effect; there is no direct relationship between number of species and the response in the species pool.

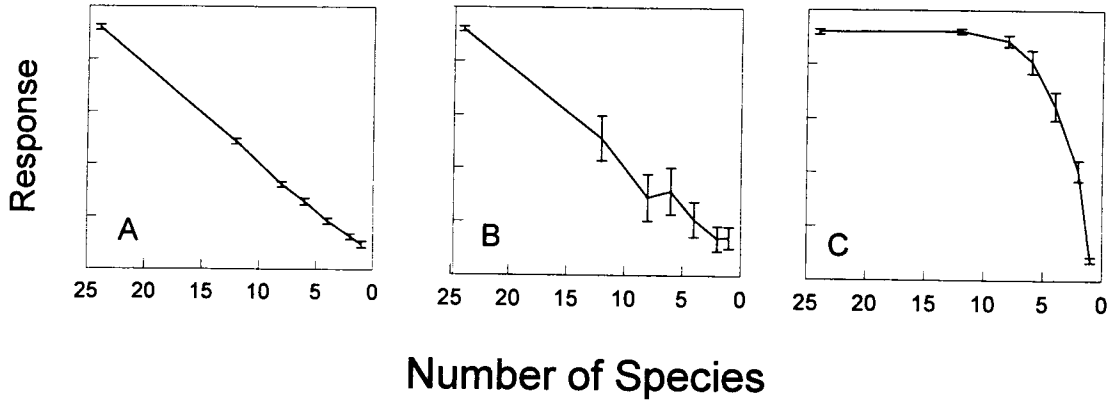

Figure 4.9. Example of an alias. An alias is a misidentification of one component of biodiversity as a different component. Example runs of three species pools sampled by design RandH. Species pools are (A) a simple additive model, (B) a simple keystone model, and (C) a group diversity model. See Table 4.2 for a description of these models. S:N ratio for all runs was 5.0 and the error bars are standard errors. Note that in (B), although variation within a treatment appears relatively small, standard deviations are actually large; this is because this experimental design has high within-treatment replication and standard error is scaled by the replication. In designs with less replication such as RandL1, that variation would probably be more evident.

Some experimental designs reduce the potential for such misidentification by allowing further inspection for correlated components. In the design used in the example above, because there are a large number of replicates in each treatment and numerous combinations of species, the keystone effect would probably be detected simply by visual inspection and the number-of-groups effect could be detected by a simple forward linear regression as the best predictor (G. Allison, unpublished data). However, this design is unique in its sheer number of sample units (Kareiva 1996) and, therefore, its ability to separate some correlated effects. Most experiments will be much more limited in power (Lamont 1995). For example, Naeem et al. (1994) were limited to 14 replicates divided into three treatments and the experiments in Chapters 2 and 3 did not have all combinations of the three manipulated groups. Furthermore, the biodiversity/response relationships are not likely to be as clean as these examples; combined effects of several biodiversity components and lower signal level will certainly muddy attempts to determine which components are most important.

SIMULATION RESULTS

For this study, I report two sets of simulations. In Series 1, nine experimental designs are compared. In these tests, the power of a design as well as the susceptibility to alias-type detection were investigated across a range of S:N ratios using forward linear regression. The species pool characteristics used in each test were, for the most part, dominated by a single biodiversity component (for example, a number-of-species effect)

and, therefore, any other components detected were aliases. In Series 2, three experimental designs were compared across a range of species pool characteristics. The designs tested had the same number of sample units and differed only in how those sample units were assigned to treatments and how the treatments were defined. In these comparisons, both the power to detect a number-of-species effect (using simple linear regression) as well as the potential for aliasing across a wide range of species pool characteristics (using forward linear regression) were investigated.

Series 1: Comparison of nine designs

In this series of simulations, I compared nine experimental designs. The designs differed in the degree of replication as well as structure (as described above). Four of the designs had a small number of sample units, three of the designs had a moderate number of sample units and two of the designs were of high replication. In each of the following tests, all nine designs were used to analyze the same species pool across a wide range of signal strength (S:N ratios). This allowed me to characterize the signal strength needed for a design to detect an effect, which is an estimate of the power of the design. Furthermore, it allowed me to evaluate whether the qualitative results of a design were consistent above that detection threshold or if they changed with signal strength. See Figure 4.8 for an illustration of the differences for an additive species effect at three S:N ratios. Qualitatively, we should expect poor detection at S:N ratios below, at least, 0.1 and reliable detection at S:N ratios above 10.

Four characteristics of species pools were investigated: a simple number-of-species effect, a strong functional-group effect, a strong single-species effect, and an "idiosyncratic" effect. In this series, the simulations tested the ability of the design to detect different components of biodiversity using forward linear regression and, thus, to determine the best predictors of the response. The potential factors in the regression model were *number-of-species*, *number-of-groups*, and the presence or absence of three groups (*group 1*, *group 2*, and *group 3*, arbitrarily represented by the same number of species in the species pools). Throughout the text, italics are used to distinguish factors detected by regression from factors that were actually the source of variation in the species pool, which are in standard font.

In the first test of this series, the species pool was comprised of species that each had the same effect on the response (a simple, additive number-of-species effect). All designs detected the proper component (*number-of-species*) at high S:N ratios and most designs detected the effect even at relatively low S:N ratios (Figure 4.10). The exceptions were designs FactL and FactM, the factorial designs, which identified the alias *number-of-groups* as important in some of the runs at moderate S:N ratios. Thus, in those cases, the experimental designs misidentify group diversity as the best predictor of the species pool characteristics. Although not apparent from the figure, these designs selected either *number-of-species* or *number-of-groups* components in every run above an S:N ratio of 0.5 but not both components; thus, the signal was detected in all cases, but just misidentified in some.

Figure 4.10. Simple additive model on nine experimental designs. Factors were detected as significant with forward linear regression over a wide range of S:N ratios. The pool of potential factors include *number of species, number of groups, Group 1, Group 2, Group 3*. Graphs depict the proportion of runs in which each factor is detected as significant ($\alpha = 0.05$) at that S:N ratio. For clarity's sake, a factor was not included in the graph if it was not significant in more than 25% of the runs in some part of the range tested.

Figure 4.11. Simple keystone model on nine experimental designs. The keystone species was a member of Group 1. See Figure 4.10 for more details.

Figure 4.12. Group difference model on nine experimental designs. See Figure 4.10 for more details.

Figure 4.13. Idiosyncratic model on nine experimental designs. See Figure 4.10 for more details.

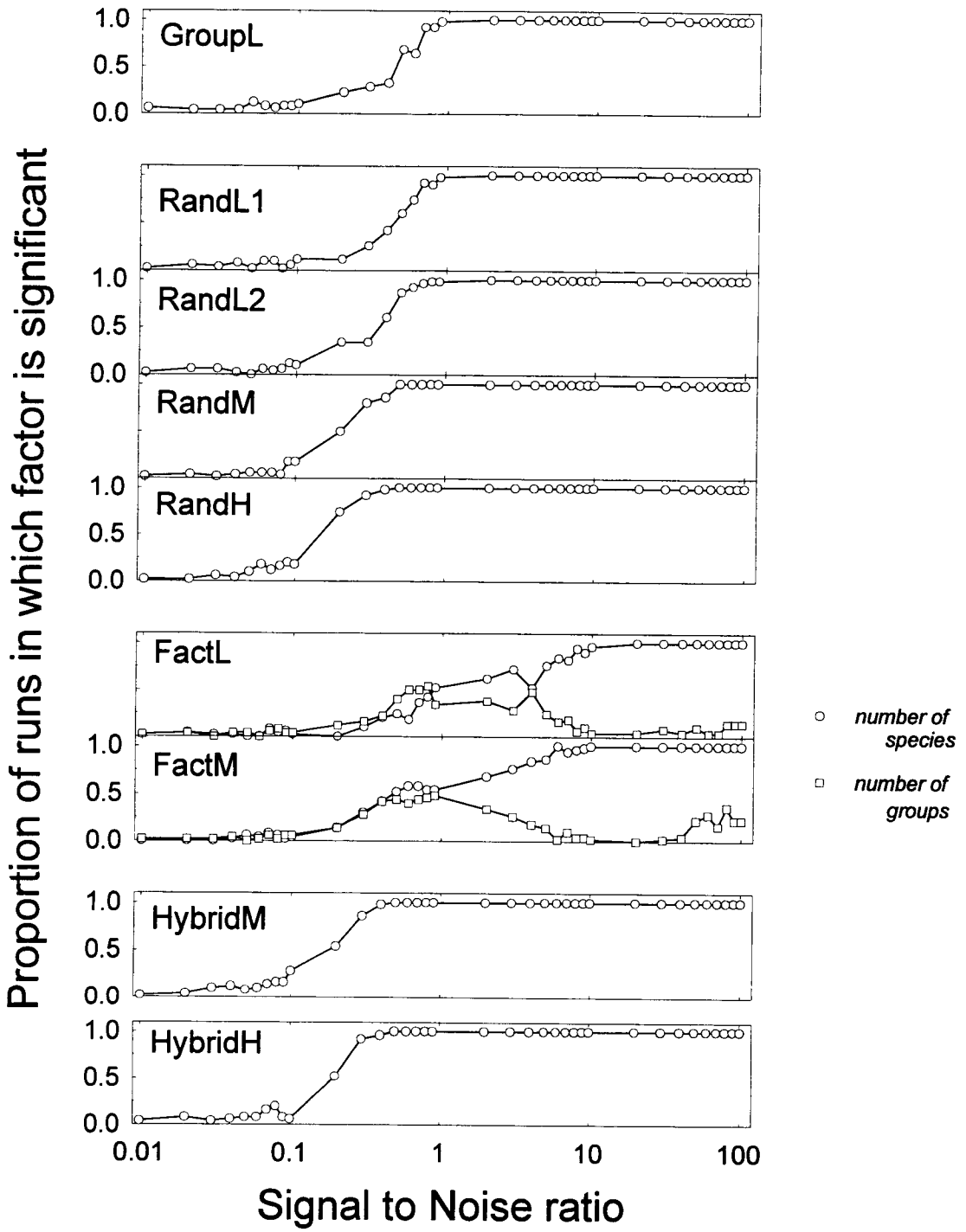
GroupL
RandL1
RandL2
RandM
RandH
FactL
FactM
HybridM
HybridH
1.0
0.5
0.0
0.01
0.1
1
10
100
Proportion of runs in which factor is significant
Signal to Noise ratio
number of species
number of groups

Figure 4.10

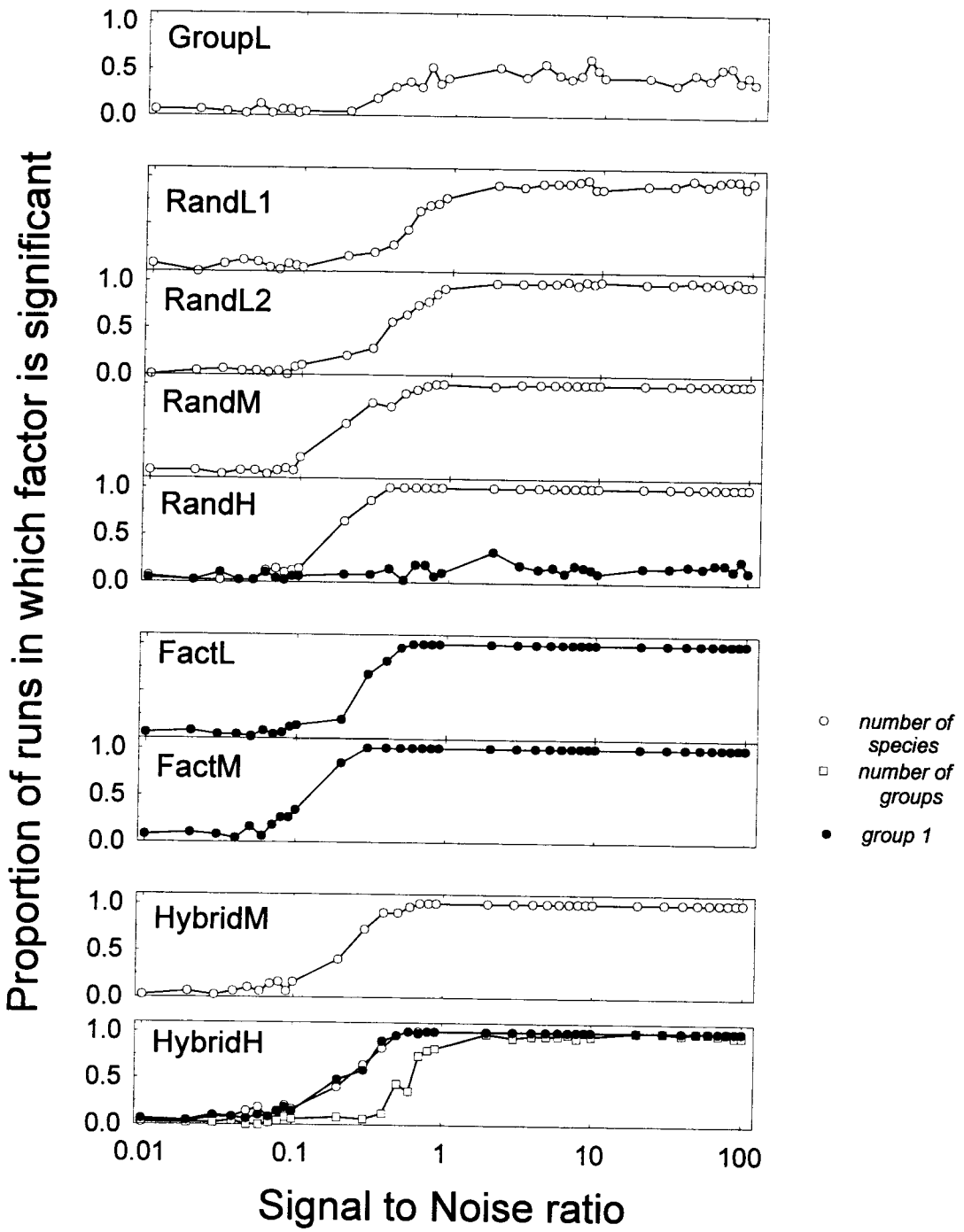
GroupL
RandL1
RandL2
RandM
RandH
FactL
FactM
HybridM
HybridH
1.0
0.5
0.0
0.01
0.1
1
10
100
Proportion of runs in which factor is significant
Signal to Noise ratio
number of species
number of groups
group 1

Figure 4.11

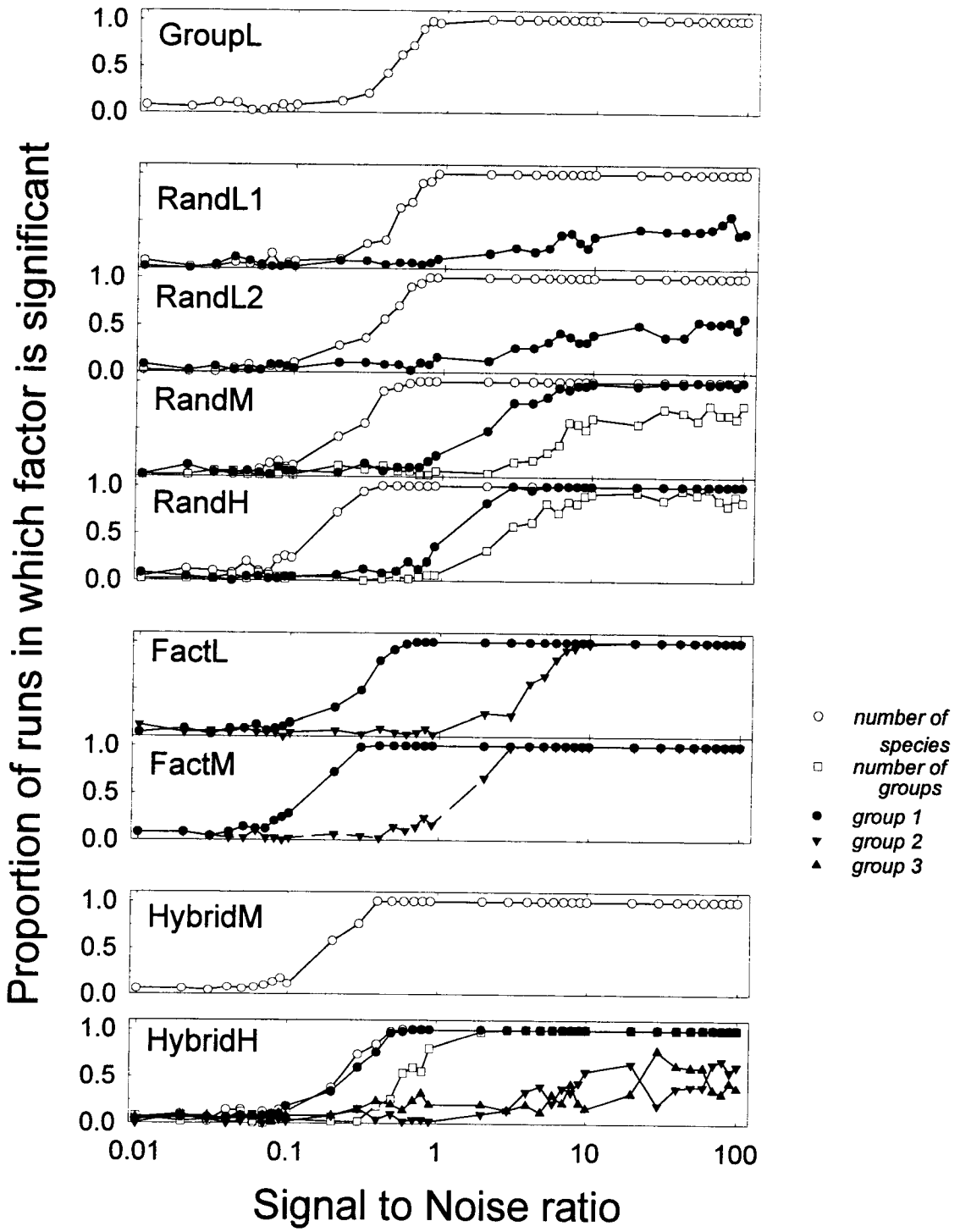
GroupL
RandL1
RandL2
RandM
RandH
FactL
FactM
HybridM
HybridH
1.0
0.5
0.0
0.01
0.1
1
10
100
Proportion of runs in which factor is significant
Signal to Noise ratio
number of species
number of groups
group 1
group 2
group 3

Figure 4.12

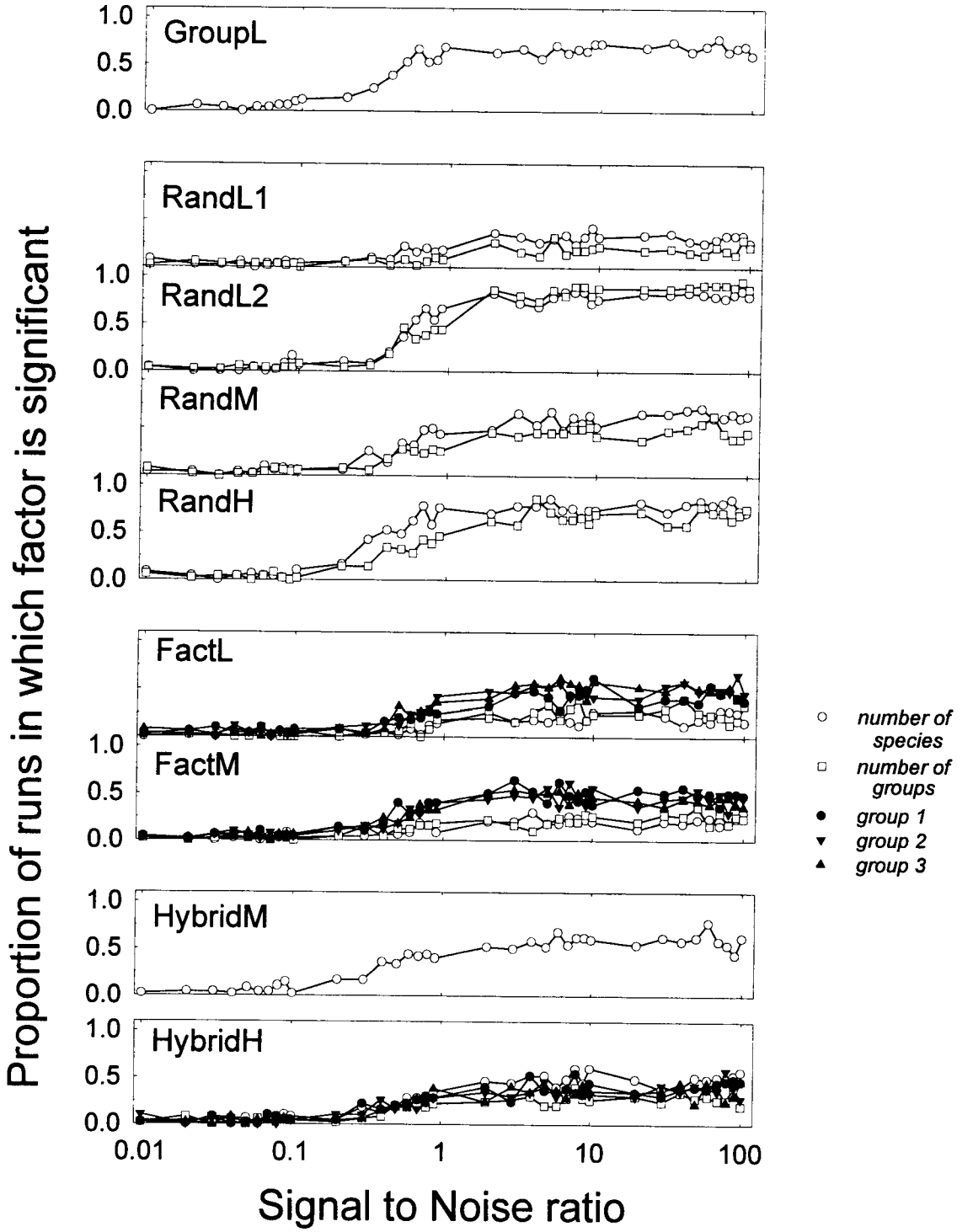
GroupL
RandL1
RandL2
RandM
RandH
FactL
FactM
HybridM
HybridH
1.0
0.5
0.0
0.01
0.1
1
10
100
Proportion of runs in which factor is significant
Signal to Noise ratio
number of species
number of groups
group 1
group 2
group 3

Figure 4.13

In the second test, a keystone effect was the only factor that influenced the response (Figure 4.11). The calculated response for each sample unit before noise was added could take only one of two values: if the keystone species (a member of group 1) was present, the response was a "1," and if the keystone species was absent, the response was a "0." The presence of all other species had no influence on the response. In this test, *group 1* represents the keystone effect because none of the experimental designs tested for the effect of a single species. Several results are noteworthy. First, only the two factorial designs (FactL and FactM) correctly identified *group 1* as the only effect at reasonable signal strengths. Second, the designs that included random species selection within a treatment for each replicate (RandL1, RandL2, RandM, HybridM, and RandH), consistently identified the alias *number-of-species* as the best predictor. This effect is obviously not a function of signal strength, because it occurs at all reasonable strengths, but rather a function of design. Third, the design that included all groups in each treatment (GroupL) did not detect the keystone effect and only unreliably detected the alias *number-of-species.* This latter result occurred because, in some cases by random selection, the keystone was included in all treatments. Also, the design HybridH, although properly detecting the keystone (*group 1*) effect, also detected the aliases *number-of-species* and *number-of-groups*. Finally, note that the difference between low and moderate replication within Rand and Fact designs is primarily a slight difference in power to detect an effect at lower S:N ratios (although not necessarily the correct effect).

In the third test, the species pool model was the functional group difference. All species in Group 1 had a strong effect on the response, species in Group 2 had a weak effect and Group 3 had no effect on the response. This species pool pattern has both a

group component and a number-of-species component because each species in groups 1 and 2 add in a linear fashion to the response. Only the factorial designs (FactL and FactM) correctly identified both *group 1* and *group 2* effects, with the strong group effect detected at lower S:N ratios than the weak group effect (Figure 4.12). However, these designs did not detect the number-of-species component of the effect. Designs that included random species selection (such as RandH) consistently identify *number-of-species* as a primary predictor of the variation in the relationship above low S:N ratios. At higher signal strength, these designs begin to identify the strong group, although not reliably in the low replication designs. And in the higher replication designs (RandM and RandH) the alias *number-of-groups* was also detected as significant. In the designs in which all groups are included in all treatments (GroupL, HybridM), *number-of-species* was the only effect ever identified as significant. And, finally, in model HybridH, although the *group 1* and *number-of-species* factors were identified correctly, the alias *number-of-groups* was identified as well, and *group 2* was not detected reliably.

An idiosyncratic effect (see Figure 4.1E) was forced by assigning a different random response value for each treatment and setting the response value for all replicates within a treatment to that same, random value. Because these treatment differences are random, any detection of effects would be aliases. In this test, all designs were more or less susceptible to this aliasing (Figure 4.13). Three points are worth noting. First, the factorial designs (FactL and FactM) tend to detect *group* effects more often than *number-of-species* or *number-of-groups*. However, for the designs that include random species selection, just the opposite is the case; only *number-of-species* and

number-of-groups are detected. Second, comparing RandL1 and RandL2, the design with only a few treatments (but many replicates within each treatment; RandL2) is more susceptible to aliasing than the design with many treatments (RandL1). This may be expected with a linear regression approach because there are likely to be more spurious linear relationships in a design with only a few treatments than one with many treatments. Finally, in a real experimental situation, consistent treatment differences caused by idiosyncratic effects are much less likely when replicates have random species assignment (such as designs RandL1, RandL2, RandM, RandH) than in designs in which all replicates of a treatment are the same (GroupL, FactL, FactM) especially if those idiosyncratic effects are due to complex species interactions. In the former designs, the within-treatment randomization of which species are present should counter some of the biases of strong, individual interactions. In Figure 4.13, I have, in effect, forced an unlikely situation in "Rand" designs.

Series 2: Comparison of moderately-replicated designs

In the second series of simulations, I tested three experimental designs in more detail than in Series 1 simulations by varying the characteristics of the species pools. These species pool characteristics include 1) the spread of the variation in an additive species effect, 2) the magnitude of differences among functional groups, and 3) the strength of a single species relative to an additive species effect. Because the character of the species pool changes as these three parameters are varied, we should expect a design

to find, as primary predictors, different biodiversity components across the range of the parameter. This will be explained further for each of the tests below.

The experimental designs were tested for two properties. The first was the power to detect a simple number-of-species effect with a simple linear regression and, thus, how well the design was able to detect **any** effect as a *number-of-species* effect. This was evaluated by determining the minimum S:N ratio in which more than 80% of the runs detected a significant regression. This was a test of the appropriateness of using a *number-of-species* effect as a surrogate for biodiversity effects in general, or at least for the biodiversity components varied in these tests. The second test was an assessment of the susceptibility of these designs to aliasing (at a S:N ratio of 5) and used the forward regression method described for Series 1 simulations. The three designs used in this series (FactM, RandM and HybridM) have the same total number of sample units and, therefore, the same experimental "cost."

In the first test, an additive number-of-species model was used and the parameter varied was the spread of species effects. Species spread merely determines the difference among species in their effect on the response. When species spread is zero, all species contribute equally to the response by a standard amount. As the spread increases, the deviation around that average amount increases.

For all designs, there was good detection of a *number-of-species* effect (minimum S:N ratio was small) in at least 80% of the simulation runs except when the species spread was large (>10) (Figure 4.14, left panels). Such high values of species spread represent a huge deviation from the average linear number-of-species effect, where some species have strong positive effects on the response, and other species have strong

negative effects. The poor and variable detection at these high values was most likely caused by strong negative effects canceling out strong positive effects (G. Allison, unpublished results). Such a pattern probably should not be labeled as number-of-species dominated but instead is dominated by unique species.

The RandM and HybridM designs reliably detected *number-of-species* as significant, with only a minor drop off of power at high species spread (Figure 4.14, right panels). At higher values of species spread, the full factorial design, FactM, detected other factors besides *number-of-species*, indicating this design was susceptible to aliasing.

Figure 4.14. The effect of species spread in a simple additive model on the detection of biodiversity effects in three experimental designs (FactM, RandM, HybridM). See Table 4.1 for descriptions. Left-hand panels illustrate the minimum S:N ratio required to detect (at $\alpha = 0.05$) the simulated relationship in 80% of the trials with a simple linear regression of number-of-species on the response. These minimum values were determined to the nearest hundredth of a S:N ratio unit. The right hand panels illustrate the proportion of runs in which factors are detected as significant ($\alpha = 0.05$) in a forward linear regression at S:N ratio = 5 (see main text). For clarity's sake, a factor was not included in the graph if it was not significant in more than 25% of the runs in some part of the range tested.

Figure 4.15. The effect of differences in functional group contribution to the response on the detection of biodiversity effects in three experimental designs. See Figure 4.14 for more details.

Figure 4.16. The effect of the strength of a single species in a simple additive model on the detection of biodiversity effects in three experimental designs. The strong species adds to the response in the same direction as other species in the pool. See Figure 4.14 for more details.

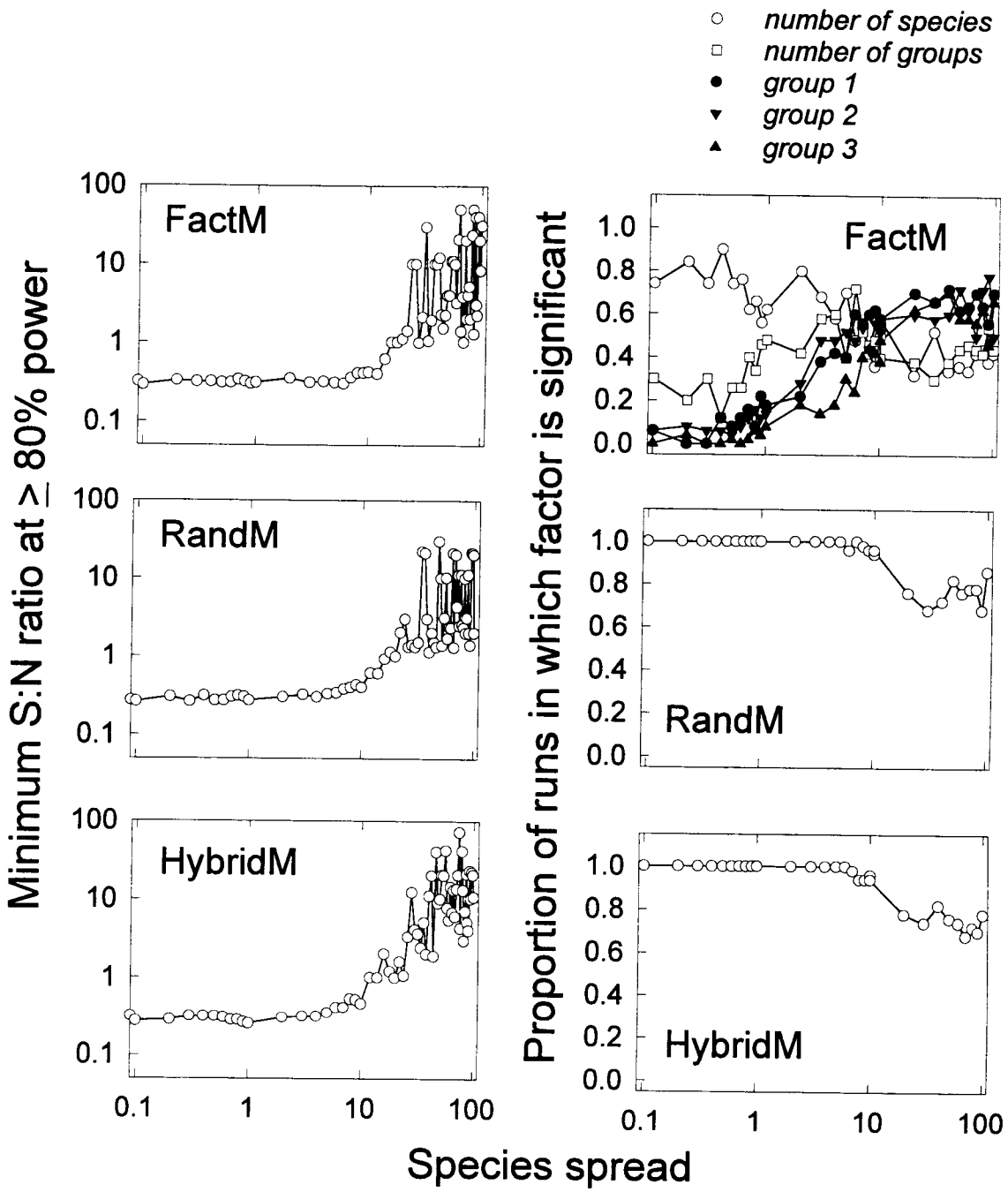
number of species
number of groups
group 1
group 2
group 3
FactM
RandM
HybridM
Minimum S:N ratio at ≥ 80% power
Proportion of runs in which factor is significant
Species spread
100
10
1
0.1
1.0
0.8
0.6
0.4
0.2
0.0

Figure 4.14

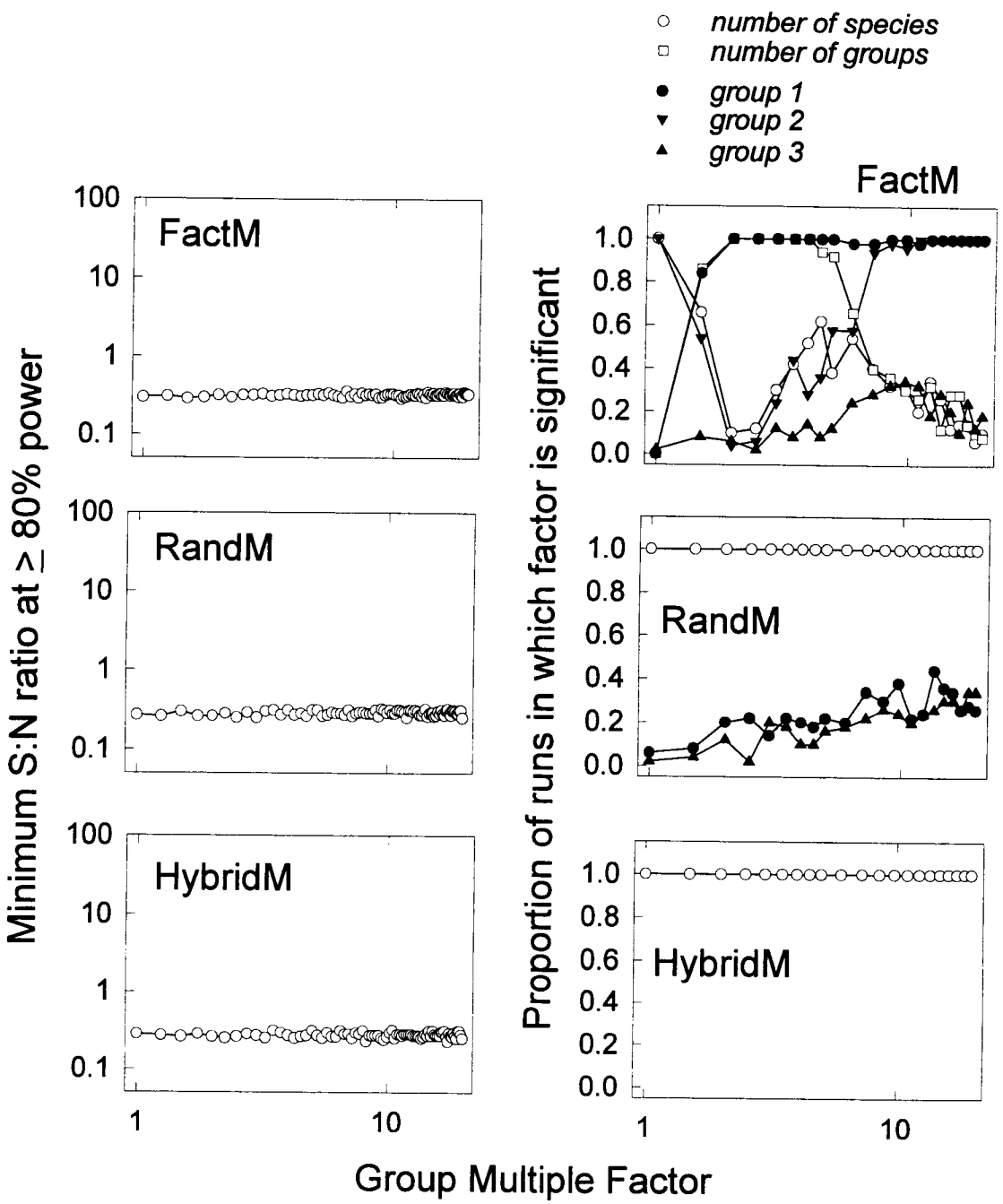
number of species
number of groups
group 1
group 2
group 3
FactM
RandM
HybridM
Minimum S:N ratio at ≥ 80% power
Proportion of runs in which factor is significant
Group Multiple Factor
100
10
1
0.1
1.0
0.8
0.6
0.4
0.2
0.0
1
10

Figure 4.15

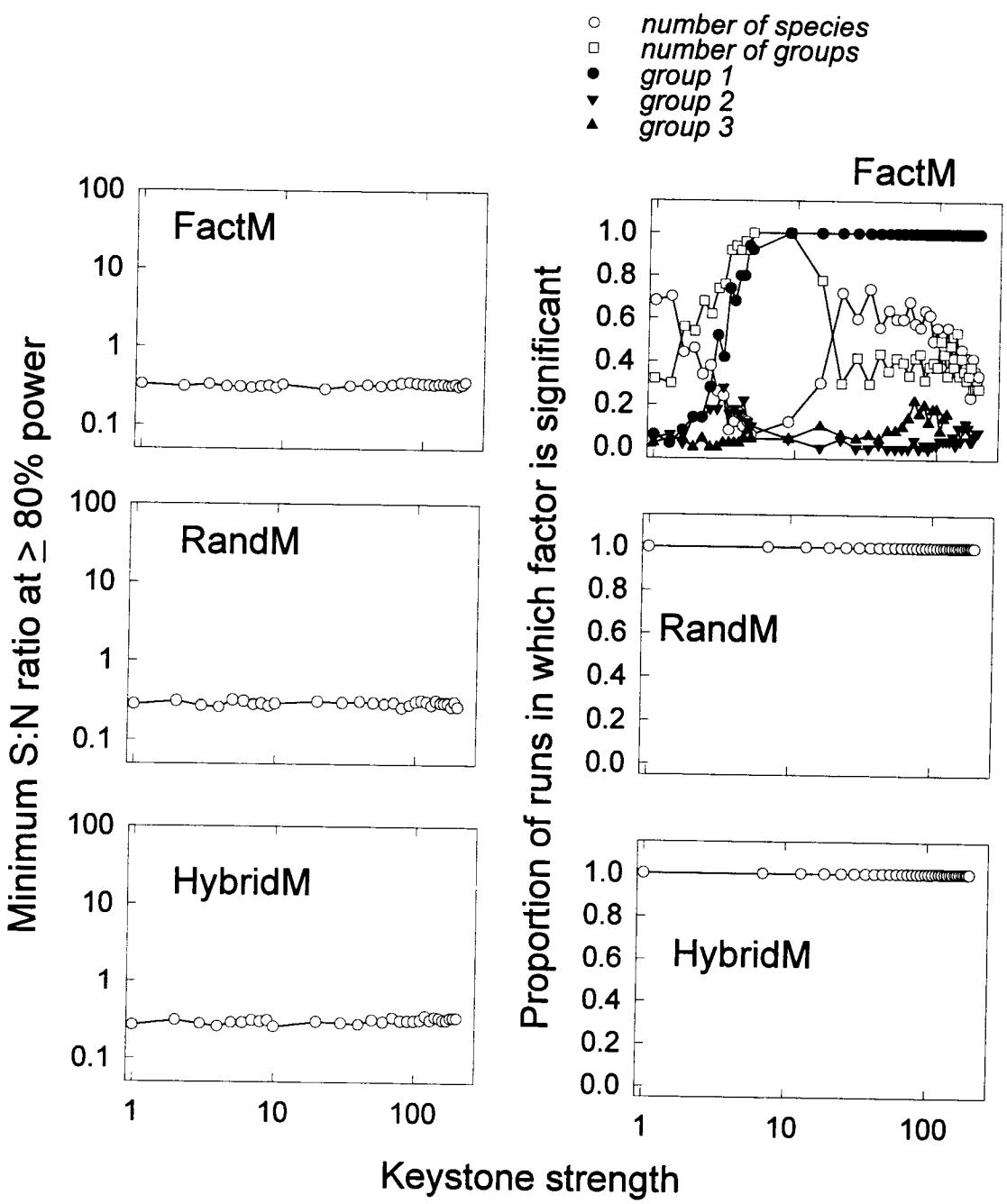
number of species
number of groups
group 1
group 2
group 3
FactM
RandM
HybridM
Minimum S:N ratio at ≥ 80% power
Proportion of runs in which factor is significant
Keystone strength
100
10
1
0.1
1.0
0.8
0.6
0.4
0.2
0.0
1
10
100

Figure 4.16

In the second test, the difference among functional groups was varied. In this situation, although there were functional group differences, there was also an intrinsic number-of-species effect because all species have an additive effect on the response. As the group-multiple factor increases, a hierarchy of group effects was created, with Group 1 > Group 2 > Group 3. All designs were sufficiently powerful (small minimum S:N ratio) to find a significant *number-of-species* effect with a simple regression model throughout the range of functional group differences (Figure 4.15, left panels). However in separating biodiversity components, designs RandM and HybridM erroneously identified *number-of-species* as the only strong predictor in the forward regression (Figure 4.15, right panels). For RandM, the lack of detection of the stronger groups occurs despite the inclusion of the *group* identifiers in the forward selection process. For HybridM, this lack of detection is expected because all groups occur in every treatment by design. Only the full factorial design, FactM, detected the functional group differences, but that only occurred reliably for both *group 1* and *group 2* at a fairly strong group difference (factor > 8). At weaker group differences, although *group 1* is identified correctly, *number-of-groups* is misidentified as a proper predictor. Furthermore, this design does not identify the number-of-species component in the signal.

In the final test, the strength of a single, "keystone" species was varied. A simple additive relationship was used with all species having an equal effect on the response (with no compensation) except the keystone whose strength was varied relative to the other species. Therefore, when the keystone's strength was set to 1.0 (on the left of each x-axis of Figure 4.16), there was a simple additive relationship between the number of species and the response (similar to that used in Figure 4.10). As the strength of the

keystone increased (moving to the right in each panel), the keystone effect comes to dominate the response. With the simple linear regression, all three designs reliably identified a *number-of-species* effect at a very low S:N ratio throughout the range of this test (Figure 4.16, left panels). However, for the identification of proper biodiversity components, the designs differed. The full factorial design FactM correctly identified *group 1* at a reasonably small keystone value (approximately 4) although *number-of-groups* was also identified except where the keystone strength was greater about twelve times other species. As explained above, none of these designs examined the effects of a single species, so the best response we can expect from these designs is a strong *group 1* effect. Nevertheless, the only consistently identified predictor in RandM and HybridM was the alias *number-of-species*.

Thus, in all Series 2 results, the designs performed well in detecting different biodiversity components as a *number-of-species* effect with simple linear regression, at fairly low S:N ratios. This indicates that the number-of-species in a system may be a reasonable surrogate for other biodiversity components, at least for those components tested here. However, in attempts to identify the appropriate biodiversity components with forward linear regression, considerable differences emerged. In particular, designs RandM and HybridM identified *number-of-species* as the predominant biodiversity component even when functional groups or keystone species were the primary source of variation. This strong alias occurred throughout the range of the variables tested. On the other hand, design FactM could reliably detect functional group effects and keystone effects (as a group effect) at the higher range values, but other effects such as *number-of-species* or *number-of-groups* were identified as important when the values

tested were in the low range. Therefore, aliasing in FactM depended upon the strength of the effect.

The main points of Series 1 and Series 2 simulations can be summarized as:

- Different designs yield different answers under identical conditions.
- Designs randomizing the species used in each replicate consistently identify all biodiversity effects as *number-of-species* effects, even when that effect is not present. Such designs with moderate and high replication also identify spurious factors when functional group differences are the primary effect.
- Designs that include all functional groups in every treatment can only identify *number-of-species* as the primary effect.
- Designs that manipulated groups are good at detecting functional group and keystone species effects, but often also identify spurious factors as significant under simple additive and idiosyncratic effects, as well as under weak group and single species effects. If the actual effect is a species number effect, these designs do not perform as well as "Rand" type designs to select that factor from other potential factors.

DISCUSSION

These simulations establish that the fundamental complexity of the independent variable in biodiversity experiments will demand attention at all stages of the research. Although more sophisticated analyses may be performed than I report, these results

demonstrate that experimental designs will vary in their power to detect investigated effects and, more importantly, in their susceptibility to misidentification of causal factors. In some cases, experiments will give consistent signals over a wide range of effects but will be unable to separate which components are the primary causes. In other cases, experimental designs may be able to separate some biodiversity components, but may be susceptible to spurious detection of other biodiversity components. Comparisons of results from different experiments must be approached cautiously, therefore, and the degree of generalizable results from any one experiment is likely to be limited.

When should aliasing be a concern? It depends on the objective of the research. If the goal of a study is to detect the presence of a relationship between biodiversity (in a broad sense of the term) and a community response (e. g., productivity or resilience to a disturbance), aliasing is potentially an asset because it increases the design's sensitivity to many components of biodiversity. Therefore, as long as interpretations are not made that suggest one component of biodiversity has more influence than another, or that a tested component is important (i. e., "diversity *per se* is important"), then alias-sensitive designs may be effective. However, numerous experiments of this type on the same response are not likely to yield extensive insights because the experiments may yield little practical predictive power. Indeed, once a relationship between biodiversity and a response has been established, the primary focus of the research should shift from *whether* there is an effect to *how* biodiversity affects the response (McNaughton 1993) and determining the primary component of biodiversity that affects the response is the next likely step.

If, on the other hand, the goal of a study is to characterize a species pool, care is necessary to prevent mis-interpretation. First, designs that are particularly alias-sensitive

should be avoided. Second, individual experiments are not likely to yield the whole picture of the species pool. If a detailed characterization of the species pool is desired, these diversity experiments are useful mostly for suggesting what to explore next. Characterizing a species pool will probably require many experiments of different types.

Aliasing effects may also confound interpretation of the shape of the relationship. In particular, caution is necessary if the shape is used to draw conclusions about species pool characteristics such as the degree of compensation. For instance, it would be misguided to characterize the species pool sampled in Figure 4.9B as linear because that response is solely a function of a single species. Shape is likely to be highly dependent on the sampling design and thus potentially very deceptive.

Because of all of these confounding problems, researchers using experiments may have an added analysis burden to convince readers that effects demonstrated in their experiment are actually attributable to the biodiversity components that the experiment indicates. For example, currently published reports (Naeem et al. 1994, 1995, Tilman et al. 1996) do not explicitly address whether results may be attributable to a small number of species (although that is certainly a possibility) and data presented are not extensive enough to allow readers to evaluate for themselves. While these studies were not necessarily attempting to separate biodiversity components, readers may erroneously draw conclusions from these studies or summaries of those studies (Kareiva 1994, 1996) that are not necessarily supported. In future studies, researchers must state the goal of the experiment and the limits of the inferences of the results.

Given these limitations, where are biodiversity experiments likely to be the most useful?

- For the objective of testing for the relationship between biodiversity (in the broad sense) and a number of important responses: Designs such as RandH (and variants) are best suited for this line of investigation because they yield a single, clear answer for a variety of different effects.
- For the objective of characterizing species pools: Experimental designs such as the factorial designs provide a first cut of how groups of species affect a response and the relative importance of each group. If more detailed understanding is required, traditional single-species manipulations could follow these experiments to identify key species (if any) and the degree of compensation within a group.
- For comparisons of biodiversity effects across environmental conditions and among sites: All types of designs are appropriate for this goal if care is used to be consistent among the tests. Another approach is to make comparisons across gradients within a single experiment (Chapter 2).

Aliasing will not be limited to experimental studies. Indeed, observational studies and indirect manipulations of biodiversity are likely to be more susceptible to aliasing than direct experiments. Because experimenters are forced to explicitly define the diversity components manipulated by their design decisions, their results can be interpreted in light of only those components manipulated. For example, experiments could control for structural diversity aliases by selecting a species pool that contains only

species with similar structural characteristics. Observational studies and indirect manipulations will face not only a larger set of biodiversity components, but also many factors that influence patterns of diversity (Chapter 1). Whenever possible, such studies should be followed by experiments to test hypothesized relationships.

The broad task of understanding the effects of biodiversity and the consequences of its loss is huge but important (Mooney et al. 1995a, Risser 1995). We are barely at the beginning stages of predicting how changes in biodiversity will affect ecosystem functioning and community dynamics in any given system. Studies such as the experiments described in this chapter hold the promise to expand our understanding of how species reductions will impact community and ecosystem properties and thus, deserve extensive attention. But the problems outlined here will impede our ability to fully answer the questions of interest. If these problems are not addressed, the potential for misinterpretation will be severe and thereby reduce the ultimate usefulness of such studies.

CHAPTER 5

General Conclusions

This dissertation has focused on experimental approaches to the topic of how diversity reductions may influence ecological properties of communities. Because direct manipulations of diversity can more clearly attribute causation to changes in diversity, such experiments will probably hold a special place in biodiversity research and in attempts to understand and predict the implications of loss of diversity.

In Chapter 2, I reported the results of a diversity manipulation press in a high zone, rocky intertidal community. This experiment demonstrated the existence of a range of interaction strengths and signs and because of that, the predicted outcome of diversity loss would be highly dependent on the identity of the species lost. Furthermore, a gradient of potential stress within the experiment was strongly modified by diversity such that higher diversity ameliorated the effects of the gradient at the harsher end. This experiment suggested that broad patterns of environmental stress and other factors that affect species interactions may be used as a rough guide to where the effects of loss of diversity will be most detrimental.

In Chapter 3, I reported the results of an experimentally-induced heat stress on different levels of diversity. Because higher diversity treatments, and especially those with the dominant algal group, the fucoids, had higher biomass before the thermal stress, they were the most affected. However, there was little evidence of a stronger proportional effect on higher diversity treatments and, indeed, an indication that high

structural diversity ameliorated proportional loss to canopy cover. Resilience to the disturbance caused by the thermal stress was greatly affected by both the degree of disturbance and the diversity of the community at the start of the recovery. In general, reduced diversity treatments recovered slowly either because of slow recovery of some species that had been excluded or because some non-typical states were persistent.

In Chapter 4, I evaluated how the choice of experimental design can influence results in biodiversity experiments. I found that a phenomenon common to all designs was the detection of an effect of one biodiversity component (e. g., a species number effect) when in fact the actual effect was caused by a different biodiversity component (e. g., a unique or keystone species). Thus, although the biodiversity effect was detected, it was mislabeled. This "aliasing" will impede our ability to perform one of the primary functions of diversity experiments, that is, to discern which biodiversity components are important.

Although experimental manipulations of diversity offer perhaps the most direct assessment of the effects of diversity, it is important to remember their limitations. Diversity experiments, because they deal with a large number of species will typically be phenomenological; determining the underlying mechanism for any diversity effects uncovered will likely require more specific experiments. Further, a number of scale issues will impinge on diversity experiments. Because experiments are typically logistically time-intensive, they will be limited in the spatial and temporal scale they can encompass. Thus, experiments will be constrained in the ability to test potential diversity effects that may operate primarily over long-time frames or large spatial expanses, such as the insurance hypothesis (the persistence of ecosystem functioning in higher diversity

systems despite environmental extremes that cause extinctions; Grassle et al. 1991, Chapin et al. 1995, Cullen 1995). Another scale issue is the potential mismatch between the scale at which diversity occurs and the scale at which potential diversity effects operate. For example, if diversity effects are the manifestation of species interactions that occur because of direct contact (say, on the scale of centimeters) but diversity occurs on larger scales (say, on the scale of meters or tens of meters), direct interactions may be rare. Experiments such as Tilman et al.'s (1996), force the effects of close proximity by planting different levels of diversity in the same sized area and thus, examine *potential* effects of diversity. On the other hand, experiments that manipulate diversity that occurs naturally (such as the experiments described in Chapters 2 and 3) may miss potential effects but evaluate whether natural associations of species actually produce diversity effects. Finally, the factors that cause high diversity in an area such as high spatial heterogeneity or environmental variability will also likely introduce a high degree of variability in the results of experiments, thus reducing the power of the experiment to detect diversity effects. For example, in the results presented in Chapter 2, the heterogeneity of desiccation potential within a single $1m^2$ plot was great enough that using the plot average of substratum angle and relative emersion index obscured the pattern that was evident at the subsample scale. However, understanding these limitations should help us design effective experiments.

Thus, to summarize the lessons from this dissertation to the larger questions of biodiversity research: There were clearly effects of diversity reductions in the experiment but the number of species was a poor predictor for the types of effects we should expect to see, because the results were highly dependent on which species were present and

which were removed. In some cases, the remaining species in low diversity treatments (the foliose-red group) were able to compensate for the loss of all the other algal species, but that came at the price of a much slower recovery to typical community states once the diversity press was removed, as well as slower recovery from disturbance.

Another lesson from this dissertation research is that biodiversity studies may be fraught with confounding factors. Although direct diversity experiments can control for the factors that influence biodiversity patterns, the complexity of biodiversity itself will demand special attention in the analysis and interpretation of results. In many cases, single experiments may be insufficient to completely answer specific questions about the biodiversity of the system being tested. Indeed, the use of the term "biodiversity" may be inappropriate in descriptions of experimental results; using the term suggests a generality with other studies when, in fact, effects may be attributable to very different causes. Such complexity must be explicitly addressed by each researcher if misinterpretation by readers is to be avoided.

While such complexity will impede our ability to make predictions about the loss of specific species without detailed understanding of the species and its community, some broader predictions may still prove useful. For example, because the interactions in this system varied over a gradient of environmental stress and the greatest effects of the species loss occurred at the harsh end of the gradient (though not for all low diversity treatments), such gradients may serve as a rough guide to where the effects of diversity loss may be most severe, especially if the predictions about how interactions vary over gradients (Menge and Sutherland 1987, Bertness and Callaway 1993), hold in many systems. Further, understanding characteristics of stresses that impinge on communities

(Chapter 3) should help us know where to expect the diversity of a community to modify the effects of a stress and where that stress will likely overwhelm any diversity effects.

In many ways this field is still in its infancy. We are still accumulating patterns of diversity. We still debate which are the most appropriate questions to guide research. We are not sure where loss of diversity will be most detrimental. And the problems of earlier research, such as the plethora of definitions and the difficulty in making concepts operational, must still be confronted. Nevertheless, the work that is currently focused on this issue promises important advances in our general understanding of biodiversity. Furthermore, the goal of understanding and predicting the ecological consequences of human-caused changes to that diversity demands concrete, empirical investigations and diversity experiments offer an important approach to reach that goal.

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Appendix

Appendix 1 - Details of Simulation Calculations

To calculate species pool characteristics and the individual response for each replicate in the simulation of Chapter 4, the following conventions and equations were used:

Variables and Parameters:

R is the response calculated for an individual replicate.

s_i is the magnitude of the effect for species i where i ranges from 1 to the number of species in a replicate.

s_k is the magnitude of the effect for species k. Species k is the keystone species and is contained in Group 1.

g_j is the magnitude of the effect of a group of species j where j ranges from 1 to the number of groups in a replicate.

t_l is the magnitude of the effect of treatment l where l corresponds to the appropriate treatment for a given replicate. All replicates within a treatment have the same effect magnitude.

ε is the random number chosen from a normalized, uniform distribution whose range is determined by the desired signal-to-noise ratio (S:N ratio) and the range of all responses within a result (before noise).

δ is a random number.

V_i is a random number chosen from a uniform distribution, centered at 0, with a range determined by the "Species Spread" variable used in Series 2 simulations. A different value is chosen for each species *i* within the species pool.

KS is the value of the parameter "Keystone Strength" used in Series 2 simulations.

MF is the value of the parameter "Multiple Factor" used in Series 2 simulations.

Model: Simple Additive

Species effect determined by:

$s_i = 1.0$ for all species

Response for each replicate determined by:

$R = \Sigma s_i + \varepsilon$

Model: Variable species spread

Species effect determined by:

$s_i = 1.0 + V_i$ for all species

Response for each replicate determined by:

$R = \Sigma s_i + \varepsilon$

Model: Simple Keystone effect

Species effect determined by:

$s_i = 0.0$ for all species except species k and

$s_k = 1.0$

Response for each replicate determined by:

$R = \Sigma s_i + \varepsilon$

Model: Keystone + Species Number effect

Species effect determined by:

$s_i = 1.0$ for all species except species k where

$s_k = KS$

Response for each replicate determined by:

$R = \Sigma s_i + \varepsilon$

Model: Group Diversity effect

Species effect determined by:

$g_j = 1.0$ if any species from Group j is present in the replicate

$g_j = 0.0$ if no species from Group j are present in the replicate

Response for each replicate determined by:

$R = \Sigma g_j + \varepsilon$

Model: Group Difference effect

Species effect determined by:

$s_i = 10.0$ for all species in Group 1

$s_i = 1.0$ for all species in Group 2

$s_i = 0.0$ for all species in Group 3

Response for each replicate determined by:

$R = \Sigma s_i + \varepsilon$

Model: Variable Group effect

Species effect determined by:

$s_i = MF$ for all species in Group 1

$s_i = MF/2$ for all species in Group 2

$s_i = 1.0$ for all species in Group 3

Response for each replicate determined by:

$R = \Sigma s_i + \varepsilon$

Model: Idiosyncratic effect

Treatment effect determined by:

$t_l = \delta$ for all replicates in treatment *l*

Response for each replicate in treatment *l* determined by:

$R = t_l + \varepsilon$