

PROJECT SUMMARY

Underlying the diversity of life and the complexity of ecology is order that reflects the operation of fundamental physical and biological processes. Scaling relationships are emergent quantitative features of biodiversity. Some of them appear to be universal, occurring in virtually all taxa of organisms and kinds of environments. They are patterns of structure or dynamics that are self-similar or fractal-like over many orders of magnitude. They can be described mathematically by power functions. They allow extrapolation and prediction over a wide range of scales. They offer clues to underlying mechanisms that powerfully constrain biodiversity. We will use the interplay of mathematical models and empirical measurements to elucidate the physical and biological principles that determine how the life history, abundance, distribution, and species richness of organisms scale with body size, space, and time. Our program of research and education involves: i) collaborations among physicists, mathematicians, geologists/hydrologists, biologists, and ecologists; ii) interactions among scientists from seven institutions; iii) cooperation between the University of New Mexico, the Santa Fe Institute, and Los Alamos National Laboratory; and iv) interdisciplinary training for graduate students and postdocs.

PREVIOUS NSF SUPPORT:

J.H. Brown: DGE-9553623 A Bio Research Training Group in Ecological Complexity (1995-2001) Co-PI's B.T. Milne, J. Rasure, M.L. Simmons, and G.C. Stevens

B.T. Milne: BSR-9910123 Self-organization of Arid Landscapes: Tests of Optimality Principles (2000-03) Co-PI's C. Restrepo, D.A. Bader, and W. Pockman

G.B. West: PHY-9873638 The Origin of Universal Scaling Laws in Biology (1999-2001)

RESEARCH PLAN

Background

The earth's surface and the living things that inhabit it are incredibly diverse. The earth presents an abiotic template of geology, physical oceanography and limnology, and climate that varies on a scale from the largest oceans, continents, lakes, and rivers to the tiniest microsites. Billions of individual organisms belonging to millions of species are distributed over the earth. They interact with each other and the abiotic conditions on time scales from microseconds to millennia and on spatial scales from a few micrometers to the entire globe. Underlying this enormous physical and biological diversity, however, is evidence of precise, quantitative patterns and processes. Examples include the latitudinal, elevational, and other gradients of species diversity, the way that species are aggregated into genera and higher taxonomic categories, the body sizes and relative abundances of coexisting species in ecological communities, the way that species diversity changes with sample area, and the successional changes in productivity, biomass, and species composition and diversity following disturbance (e.g., Williams 1964, MacArthur 1972, Brown 1995).

These emergent general features of ecological systems provide powerful clues to universal principles that constrain ecological complexity and regulate biodiversity. On the one hand, the emergent patterns represent the outcome of the fundamental law-like processes of physics, chemistry, and biology. Many of these mechanisms are well understood. They include thermodynamics, conservation of mass and energy, atomic particles and chemical elements, chemical stoichiometry, geological tectonics and erosion, laws of biological inheritance, evolution by natural selection, and many others. On the other hand, there remains the challenge of elucidating how these fundamental processes give rise to ecological systems that are simultaneously extremely diverse and highly constrained. Most of the emergent ecological phenomena mentioned above have been recognized for decades and sometimes for centuries. Nevertheless, theoretical explanations in terms of basic physical and biological principles have remained elusive.

Our proposal focuses on one restricted class of emergent ecological phenomena: scaling relationships that are self-similar or fractal-like over a wide range of spatial or temporal scales. At least some of these relationships appear to be universal: they apply to plants, animals, and microbes; to terrestrial, marine, and freshwater habitats; and to human-dominated as well as "natural" ecosystems. Current research, much of it by our group, is revealing the mechanisms. Scaling relationships result from powerful constraints on the organization of complex systems – constraints that are consequences of a few basic physical, biological, and mathematical principles. Structures and processes that are self-similar over many orders of magnitude provide a means for extrapolating between scales: between the large scale of the globe, region, ecosystem, or habitat where ecological relationships appear to be complex, and the small scale of

the field or laboratory experiment where hypotheses can be tested and mechanisms can be documented. Most importantly, the study of scaling is one powerful way of simplifying ecological complexity and of understanding the physical and biological principles that regulate biodiversity.

Scaling relationships offer several advantages for theoretical analysis and empirical investigation.

First, they can be characterized mathematically by an elegantly simple form, the power function, $Y = Y_0 X^b$, where Y is a dependent variable, Y_0 is a normalization constant, X is the independent variable, and the exponent b is another constant. Taking the logarithms of both sides of this equation gives the expression for a straight line, so the statistics of linear regression can be used to fit power functions to data (Fig. 1). The term allometric equation is used for power functions describing dependence of biological variables on body size.

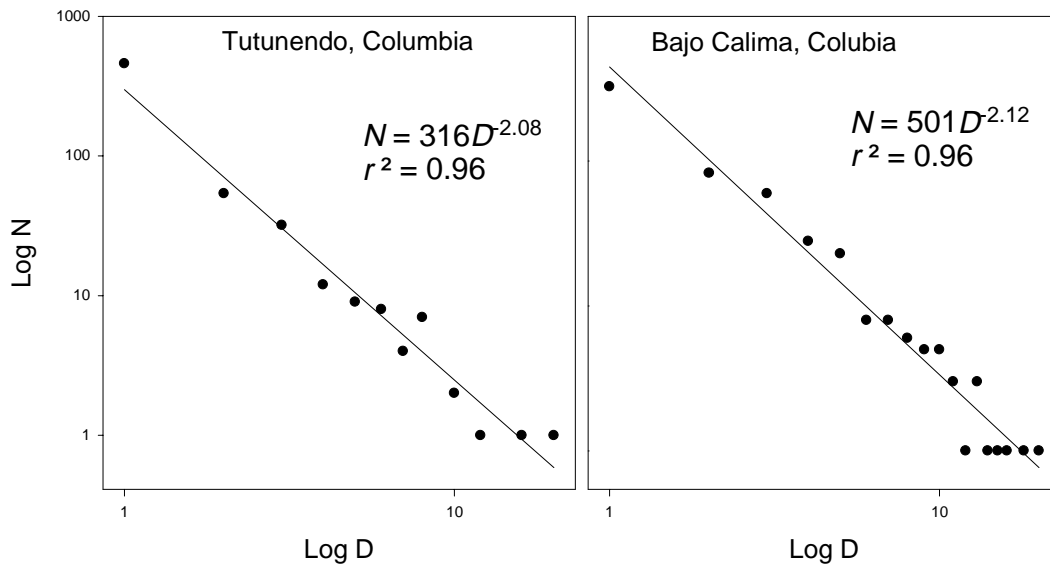


Fig. 1. Relationships, plotted on logarithmic axes and fitted with power functions, for number of stems (N) as a function of trunk diameter (D) for all of the trees in two 0.1-ha plots of tropical rain forest in Columbia: left: Tutunendo with 590 individuals of 271 species and right Baja Calima with 556 individuals of 263 species. Note the goodness of fit of the power function (regression lines) and the similarity of the exponent to the predicted value of 2.0 (data: Gentry database; analysis: Enquist, Brown, and West unpublished).

Second, many scaling relationships are highly constrained. Statistical fits to data are often so precise that the resulting equations are referred to as scaling laws. So, for example, we have the Gutenberg-Richter law relating the frequency and magnitude of earthquakes, Kleiber's law relating metabolic rate to body mass in animals, Taylor's power law of population fluctuations, and Yoda's thinning law relating density of stems to plant size. The precision of these relationships suggests that they are constrained by fundamental mechanisms, and the values of the constants, Y_0 and b , offer valuable clues to the identity and mode of action of these underlying processes.

Third, while some emergent ecological phenomena cannot be described by power functions,

scaling relationships are widespread. Work on fractals is filled with examples from ecology, biology, and the earth sciences (Mandelbrot 1983). Examples of ecological data that have been fit with power functions include numbers of species within genera or higher taxonomic categories (Burlando 1990, 1993), magnitudes of fluctuations in populations (e.g., Taylor 1986, Keitt and Stanley 1998), influence of body size on diet, life history, and population density (e.g., Yoda et al. 1963, Peters 1983, Calder 1984, Reiss 1989, Charnov 1992, Enquist et al. 1998, 1999; Ritchie 1998, 1999), fractal-like patterns of plant structure (Morse et al. 1985) characteristics of stream networks and other landscape features (e.g., Gupta and Waymare 1989, Milne 1992, 1998, Rodriguez-Iturbe and Rinaldo 1997), and species-area and species time relationships (e.g., MacArthur and Wilson 1967, Rosenzweig 1995, Harte and Kinzig 1997, Harte et al. 1999). These empirical equations imply that the scaling is powerfully constrained, and the fitted values of the constants reflect the operation of fundamental mechanisms. Fourth, similar scaling relationships are found in other complex systems, from physical particles and geological structures to human economies and languages. One consequence has been interdisciplinary communication and collaboration, the development of shared vocabulary and methodology, and the search for a unifying conceptual framework. Scaling relations have served as one focus of the interdisciplinary sciences of complexity as practiced at the Santa Fe Institute and elsewhere (e.g., Lewin 1992, Waldrop 1992, Gell-Mann 1994, special report in the April 2, 1999 issue of *Science*). Concepts and methodologies developed in other disciplines can be applied to ecology and vice versa.

And finally, we have assembled collaborating scientists and institutions with exceptional expertise in this area. The Santa Fe Institute (SFI) and Los Alamos National Laboratory (LANL) pioneered interdisciplinary studies on complex systems. The University of New Mexico (UNM) used its own resources and the “SFI-LANL connection” to become a recognized center of research and graduate training in several areas of ecological complexity. These activities were greatly facilitated by a NSF Graduate Research Traineeship (GRT) grant in “ecological complexity.” Interdisciplinary collaborations have increased as the accomplishments have attracted both senior and junior scientists.

Conceptual Framework and Research Goals

Our proposed research is based on three premises: i) scaling relationships, power functions, and fractals provide a powerful analytical framework for investigating universal principles that govern the structure and dynamics of complex ecological systems; ii) scaling relationships offer clues to how the laws of physics and chemistry and the fundamental processes of organismal biology give rise to emergent features of biodiversity; and iii) one productive way to investigate scaling relationships and the physical and biological bases of biodiversity is through continued interdisciplinary collaboration.

i) Power functions

Power functions have been used to describe three classes of phenomena. Placing ecological scaling relationships into one of these classes clarifies the nature and domain of self-similar behavior and facilitates the search for underlying mechanistic principles.

The first class includes those where the constants take on only a limited range of values. Of particular interest are values of the exponent, b , which are often simple multiples of a number. For example, phenomena that exhibit Euclidean geometric scaling have exponents that are

multiples of $1/3$ when the independent variable, X , is mass (M) or volume (V): i.e., linear dimensions scale as $V^{1/3}$ and surface areas as $V^{2/3}$. In contrast, biological allometries tend to scale as quarter powers of mass: whole organism metabolic rate scales as $M^{3/4}$; development time, lifespan, and other biological times as $M^{1/4}$; and heart rate, maximum rate of population growth r_{max} , and other rates as $M^{-1/4}$ (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Charnov 1993). The constrained values of the exponent can provide invaluable clues to the fundamental processes that govern the scaling behavior. Thus, for example, the pervasive quarter-power scaling in biology apparently reflects the fractal-like designs of resource distribution networks (West et al. 1997, 1999a,b).

The normalization constants, Y_0 , can also provide clues to underlying mechanisms. For example, in biological allometry, values of Y_0 often differ among taxa of organisms and environmental settings. They appear to be related to fundamental constraints on the system: i) differences among taxa in whole-organism power or production and in its differential allocation to maintenance, growth, and reproduction; and ii) differences among environments in the availability of energy, nutrients, or other essential resources. For example, Y_0 for growth in diameter differs among coexisting tree species in a tropical forest, but much of this is due to variation in wood density, and the rate of carbon allocation to growth is actually quite similar among species (Enquist et al. 1999).

The second class of ecological scaling relationships is not so constrained. In empirical equations the constants, Y_0 and b , take on a wide range of values. For example, a power function gives a close fit to the relationship between variances and means of the time series for population densities of a single insect species at multiple, spatially separated sites (Taylor 1986, Taylor et al. 1980). But different species have statistically different values of Y_0 and b . Brian Maurer (pers. comm.) obtains similar results for time series data for North American bird species. Such variable scaling relationships may reflect mixtures of lognormal distributions with different variances (Allen, Li, and Charnov submitted). Li et al. (1992) introduced a simple mathematical transformation based on weighted variances to form a stable distribution from combinations of such mixed distributions. Magnitudes of variation in species-specific parameters determine the values of Y_0 and b .

At first glance, such relatively unconstrained power functions may seem to offer few clues to specific physical and biological mechanisms. The possibility exists, however, that most of the variation is due to some key process, which can be characterized in terms of a parameter or combination of parameters. One example is the way that the Reynolds number can be used to reduce three key parameters of fluid flow (viscosity, path length, and velocity) to a single key variable in studies of biomechanics and allometry (e.g., Koehl 1995, 2000).

The third class of ecological scaling relationships may not represent examples of self-similar behavior over a wide range of scales. Examples may include species-area and species-time relationships and distributions of abundances or body sizes among species within a community. There is a long tradition of fitting species-area data with power functions (e.g., Willis 1922, Preston 1962, MacArthur and Wilson 1967, Rosenzweig 1995; Hubbell 1995, in press). Some authors have suggested, however, that these relationships tend not to be self-similar over many orders of magnitude (e.g., Williams 1964, Connor and McCoy 1979, Brown 1995, Rosenzweig 1995). There is also a question of whether exponents of species-area relationships vary widely or tend to take on a particular value, such as $1/4$. In the case of species-abundance distributions, it is

known that the data often are at least as well fit by other mathematical distributions as by power functions (see discussions in Whittaker 1970, May 1975, Tokeshi 1990).

ii) Physical and biological bases of biodiversity

Biodiversity poses one of the greatest challenges to modern science. Can the variety of living things and ecological systems be explained in terms of relatively simple laws or principles? We are optimistic. We see evidence for such principles in the emergent general features of biodiversity, including the patterns of self-similarity that have often been referred to as "scaling laws." In our view, such "scaling laws" are mathematical descriptions of important patterns in nature. But they are not scientific laws, because they do not describe the processes or mechanisms that give rise to the patterns. The spiral patterns of stars in a galaxy or water in a drain are not physical laws but the emergent outcomes of physical laws operating in complex systems containing many particulate interacting components. Similarly, we hypothesize that ecological scaling relationships reflect the outcome of underlying laws. Our goal is to search for universal principles of ecology that arise from the laws of physics, chemistry, and biology. We can best illustrate our approach with examples. One is our work on allometry. Not all biodiversity is a matter of size, but size is undoubtedly one of the major axes of biological variation. Living organisms range in body mass over an amazing 21 orders of magnitude, from 10^{-13} g bacteria to 10^8 g whales. For nearly a century biologists had sought an explanation for the pervasive quarter-power allometric scaling, not only of metabolic rate, but also of many other anatomical, physiological, life history, and ecological characteristics of plants and animals. West et al. (1997, 1999a,b,) have developed models that explain these uniquely biological quarter-power scaling relationships in terms of organism-level structure and function, physical principles, and geometric design. Because of the central role of metabolism in determining resource uptake from the environment and resource allocation to maintenance, growth, and reproduction, it is possible to extend these models to account for the scaling of such ecological phenomena as population densities and growth rates of trees in forest stands (Fig. 1; Enquist et al. 1998, 1999). A second example comes from our work on river networks. Much of global biodiversity can be attributed to spatial variation in abiotic conditions and biotic interactions. The heterogeneity of terrestrial landscapes is due largely to tectonic and erosional processes that generate landforms and drainage basins. Classic scaling relationships have been described for river networks. Variations of flows, velocities, depths, widths, and slopes take the general form $Y \propto Q^b$, where Y is the hydraulic-geometric variable, Q is stream discharge and related to size of a basin, and b is a scaling exponent (Leopold and Miller 1956, Ibbitt et al. 1998). The similarity of biological and river networks and the applicability to river systems of the three assumptions of West et al. (1997) motivates our collaboration. For example, their assumption of a self-similar (fractal) vessel network corresponds exactly to the law of stream numbers described by Horton (1945) more than fifty years ago. Recent analyses of medium to large river networks find empirical bifurcation ratios, R_b , between 4.1 and 4.7 (Peckham, 1995), which are in contrast to the well-known random model where $R_b = 4.0$. We have a self-similar statistical theory to explain this feature (Veitzer and Gupta 2000). However, we hypothesize that an allometric derivation of R_b is also needed. The second assumption of invariant capillary diameter has its parallel in the well-known Horton relationship where drainage density, D , is independent of the contributing drainage area, A . However, D varies systematically with the P-E index of net moisture influx, which compares precipitation and evapotranspiration (Abrahams, 1984). Since flow from the

contributing area determines the size of first order channels, we can infer that the size of first-order channels for regions of similar P-E index are invariant with respect to basin size. Finally, the assumption of minimum stream power for the entire network, similar to West et al.'s (1997) assumption of minimum hydrodynamic resistance, has been used to predict fractal scaling exponents for river networks (Rinaldo et al 1992, Rigon et al. 1993, Sun et al. 1994). But Maritan et al. (1996) have shown analytically that this global minimization condition by itself does not explain the observed fractal exponents. Similarly, our preliminary calculations show that the assumption of branching self-similarity combined with dimensional analysis belongs to the mean-field universality class for optimal channel networks (Maritan et al. 1996). Because the mean field predictions don't agree with data, we infer that appropriate biophysical constraints must be incorporated in order to develop a correct allometric scaling theory of river networks.

Implicit in these two examples and our proposed research (below) is optimism that the emergent general features of ecological systems can be explained in terms of some basic physical, chemical, and biological principles. We will focus on the principles that may explain certain universal patterns of biodiversity: the scaling of abundance, distribution, and species richness with space, time, and body size. Knowledge of how human activities scale will clarify the threats to biodiversity, knowledge of how physical and biological processes determine the scaling of biodiversity can be used to mitigate these threats.

iii) Interdisciplinary collaboration

Our third goal is to increase interdisciplinary interaction and collaboration in both research and education. In order to pursue questions about ecological scaling relationships and biodiversity, it is desirable if not essential to incorporate general perspectives, theoretical constructs, factual information, and methodological tools from other disciplines. In our experience, the most effective way to do this is through interdisciplinary collaborations. These are not easy to form.

It is essential to find scientists who are interested in common questions, willing learn to speak each other's language, and able to trust, respect, and like each other. But when these obstacles have been surmounted, the rewards are enormous. Together we can do a kind and quality of science that none of us could do on our own.

In particular, research on "ecological complexity" at the University of New Mexico UNM) has benefited greatly from interactions with the Santa Fe Institute (SFI) and Los Alamos National Laboratory (LANL), mainly supported by the GRT in ecological complexity. Brown and Wagner are members of SFI's "external faculty" and the other UNM ecologists have participated in symposia, workshops, and more informal discussions at the Institute. SFI pioneered interdisciplinary approaches to the sciences of complexity (e.g., Lewin 1992, Waldrop 1992; Kaufman 1993, Gell-Mann 1994, Holland 1995). As hinted at above, scaling relations and other emergent features of ecological systems have intriguing parallels in other complex systems, from spin glasses and geological processes to metabolic networks and human brains to cities and economies. There has been much debate about whether such similarities are just oversimplified analogies, or whether they reflect the influences of common classes of mechanisms (Gell-Mann 1994, Anderson 1994, special April 2, 1999 issue of *Science*). Nevertheless, there is much to be gained by sharing conceptual perspectives, empirical information, and methodological tools. So we will continue existing collaborations: among Brown, West, and Charnov; Milne, Gupta, and Restrepo; Gosz, Li, Over, and Wu; and Wagner and Fell. We will form new collaborations as indicated below or as new opportunities arise. The number of institutions from which

collaborators are drawn is impressive: University of Colorado, Los Alamos National Laboratory, Texas A & M University, and Texas Tech University, in addition to UNM and SFI. We will also continue to recruit graduate students and postdocs with exceptional promise but unusual backgrounds, and encourage them to develop their own collaborative research projects. We recognize that the large number of collaborators and students with widely varying backgrounds and interests may cause this proposal to appear “diffuse.” In response, we would point to the unique mix of scientists that has self-organized to form the informal “ecological complexity group” centered at UNM, SFI, and LANL. We would also point to our accomplishments, especially to our publications on ecological complexity, scaling relationships, and related topics (see c.v.’s). We think we are doing a special kind of collaborative, interdisciplinary science.

Activities and Procedures

The proposed research will consist of two integrated components: theoretical modeling and empirical evaluation. Here we present, first an overview of these activities, then specific examples and protocols, and finally a timetable.

i) Overview

We want to build and test models that elucidate the general mechanisms that regulate biodiversity and determine the structure and dynamics of complex ecological systems. The focus will be on ecological scaling relationships. It is important to distinguish between fitting a statistical “model,” such as a power function, to data, from building an analytical mathematical model that seeks to explain the power function in terms of underlying biological, physical, and mathematical principles. While we focus on the latter, we recognize the essential role of the former. In fact, good science is an iterative series of inductive and deductive exercises: collection and analysis of data reveals empirical patterns that inspire theories and hypotheses about mechanisms; ideas about mechanisms, formalized in quantitative models, suggest empirical tests requiring collection and analysis of new data. We will use analytical models to build theories about mechanisms, and statistical models fitted to data to both inspire and test the theory.

Our theoretical modeling effort has special features. First, the models invoke fundamental mechanistic processes. They start from a few basic assumptions and seek to maximize some physical or biological quantity such as free energy, power, efficiency, or Darwinian fitness. Second, they characterize structure and dynamics of entire complex systems. Two useful techniques are i) to assume that the power functions reflect the existence of physical fractal-like components, which are incorporated explicitly into the model; and ii) to demand adherence to known conservation principles (e.g., conservation of mass, which requires accounting for the quantity of water taken up by a plant or falling on a river basin). Finally, our models are designed to be parameterized with realistic values and tested with real data. Flaws in thinking are readily revealed when the models fail to reproduce realistic values as reported in the extensive literature of ecological scaling relationships (e.g., Williams 1964, Peters 1983, Calder 1984, Reiss 1989, Rodriguez-Iturbe and Rinaldo 1997).

There are two ways that we use empirical information to evaluate models. Often a model makes precise quantitative predictions that can be tested with new kinds of data that played no role in the development of the model. For example, our allometric model for thinning not only

predicted a $-4/3$ scaling for stem density as a function of plant mass (M), it also predicted that productivity of ecosystems should be invariant (scaling as M^0) whereas biomass should increase with plant size (scaling as $M^{1/3}$). To evaluate these new predictions, it was possible to go back to the literature and compile new kinds of data to evaluate these additional predictions (e.g., Enquist et al. 1998). Predictions about population dynamics can be evaluated using long-term data bases, such as the time series of censuses from the Breeding Bird Survey or Brown's Portal LTREB site (Maurer 1998, Keitt and Stanley 1998, Stenseth and Brown in prep.). Predictions about parameters of vegetation patches or landslides can be evaluated by collection and analysis of aerial photography or satellite imagery (Milne 1998, Restrepo et al. in prep.).

Other tests of model predictions involve performing controlled, manipulative experiments or at least making new empirical measurements. While many of the questions that we address involve spatial and temporal scales where experiments are impossible, impractical, or immoral, this is not always the case. Sometimes, the critical experiment actually has already been done, but was not designed to test the model. For example, a crucial test of West et al.'s (1999) model for the plant vascular system is how resistance changes with level of branching in a tree. Yang and Tyree (1993) measured how resistance declines as successive levels of branches are removed, and their results precisely match the model predictions. Long-term field experiments, such as those at LTER or LTREB sites, provide potentially valuable tests of predicted responses to perturbations over long time scales. A priori experimental tests are possible, especially if creative designs are used to reduce the spatial and temporal scales to manageable ranges, as in microcosms, for example. Examples of ongoing or proposed experimental tests are given below.

Quantitative description of empirical phenomena and empirical tests of model predictions inevitably raise statistical concerns about independence, accuracy, and uncertainty. We are sensitive to these issues. We not only have an established track record for doing rigorous empirical ecology and comparing models to data, we also have developed new statistical techniques for analyzing data and testing hypotheses (e.g., Li et al. 1992, Brown et al. in press). Two members of our group, Milne and Li, have expertise in statistics and its mathematical underpinnings, and teach courses on applications of statistics to ecology. One advantage of focusing on power functions, mentioned above, is that simple bivariate linear statistics can be applied to log-transformed data. It is straightforward to determine whether the confidence intervals for empirical values of b or Y_0 include a theoretically predicted value. Further, the ability to collect and analyze many data points spanning several orders of magnitude gives considerable statistical power. The kinds of data that we use do raise some complicated and still controversial statistical issues: influence of spatial and temporal autocorrelation and phylogenetic relatedness on independence of data, choice of regression models, problems of estimation and model validation at the tails of distributions where data may be very sparse, and so on. We will continue to work on these issues. Statistics, like ecology, is an evolving discipline, and insistence on a rigid statistical orthodoxy is neither good for ecology nor good statistics.

ii) Specific research projects

a) Brown, West, and Charnov: life history and ecological consequences of biological allometries
Variation on body size is one of the most conspicuous features of biodiversity. Nearly all characteristics of organisms are correlated with body size, and many scale as quarter-power exponents of mass. West, Brown, and Enquist have developed a new theory for these pervasive quarter-power allometric exponents (West et al. 1997, 1998, 1999). Values of b that are simple

multiples of $\frac{1}{4}$ are hypothesized to result from the fractal-like structure and function of biological distribution networks and exchange surfaces. Now the question is, how do the geometric, physical, and biological principles of allometric scaling at the level of individual organisms influence higher levels of biodiversity. Working primarily with plants, we have made some progress: developing an alternative resource-based mechanistic explanation for the relationship between abundance and plant size, predicting variation in ecosystem biomass and productivity as a function of plant size, and accounting for the observed scaling of size structure, production, and growth in forests (Enquist et al 1998, 1999).

Current research focuses on i) continued collaboration with Enquist to model the dynamics of mixed-species forest stands and compare results with the Gentry database (Missouri Botanical Garden: <http://www.mobot.org/>) and other sources; ii) developing detailed first-principles allometric models of ontogenetic growth; and iii) using allometric data to make inferences about the evolution of energetic power and efficiency as reflected in the phylogenetic histories of major lineages. For example, the models of forest dynamics based on resource use of individual plants predict how stem density should scale as a function of plant mass (M) or diameter (D): as $M^{-3/4}$ and D^{-2} . Data from approximately 200 forests in the Gentry database generally support these predictions: regardless of latitude, species composition, and species richness, number of stems scales very closely as D^{-2} (Fig. 1). The few forests that do not conform appear to be early-successional stands that clearly violate the model's assumption of a steady-state size structure. Future research will tackle the most challenging problem: the influence of body size on species diversity (e.g., May 1986).

Future research will also address the influence of body size on life history diversity. Charnov (1993) developed much of current allometric life history theory at a time when there was only limited understanding of the mechanisms underlying scaling of metabolism, growth, and reproduction. Now it should be possible to develop more mechanistic models that can account for size-related variation in such life history components as development time, lifespan, and allocation to reproduction. Charnov also has extensive experience using evolutionary life history theory to predict the values of exponents, some of which appear universal, for non-allometric scaling relationships and behavioral rules (Charnov and Downhower 1995, 1998, Charnov and Parker 1995, 1999, Charnov 1997).

b) Milne, Gupta, Restrepo, Paczuski: Biophysical allometric-scaling theory for landscapes and river networks

The long-term objective of this research is to develop a new "allometric-hydrologic scaling" theory of landscapes which can unify diverse observations from meteorology, hydrology, geomorphology, and ecology for medium to large drainage networks. The striking similarity between river networks and biological networks suggest that similar mechanisms underlie their allometric scaling. But a theoretical formulation of hydrologic-allometry will require comprehensive empirical and theoretical understanding of water balance in river networks. Unlike a circulatory system, the fluid volume of a drainage basin varies in time and space. We define allometric-hydrologic scaling to mean the existence of empirical power functions relating hydrological, ecological, topographical, and atmospheric variables to the mass of water being transported in drainage networks. A major recent advance is a new analytical model that predicts realistic empirical values of R_b above and below 4 (Veitzer and Gupta, 2000). Moreover, in developing this model, the fundamental assumption of topologic randomness that underlies the

classic Shreve (1967) model is replaced with the assumption of statistical self-similarity. Our methods for computing hydraulic-geomorphic exponents will include a renormalization group approach as a generalization of dimensional analysis (Barenblatt 1996) with respect to those dimensionless numbers which go to infinity or to zero. This approach entails the introduction of new scaling exponents which must be ascribed biophysical meaning because they cannot be obtained from dimensional reasoning (Barenblatt, 1996). We hypothesize that the scaling exponents relate to two fundamental roles of plants in the formation of terrain. First, plants affect water balance via evapotranspiration at rates governed by allometric scaling (Enquist et al. 1998). Second, rooting strength affects erosion by regulating shear stress. Erosion creates complex terrain surfaces that regulate plant resource supply. Differential rooting of plant species on complex terrain reflects the underlying variation in resource supply (Whittaker 1967, Tilman 1982) and feeds back to affect terrain formation (Milne 1998b). Thus, we conjecture that the energy minimization in stream networks stems from the feedback between terrain and biota. This approach will provide a basis for investigating how vegetation characteristics, biological diversity, and ecosystem processes interact with, and are constrained by, the landscape (see Johnson et al. 1992, 1995, Keitt et al. 1997, Kerkhoff et al. 2000, Milne 1991, 1997, Milne et al. 1992).

Empirical validation of our theory will entail two activities: i) developing integrated data that characterize water balance of entire river networks, and ii) using these data sets to derive empirical allometric-hydrologic scaling relationships that can be compared to theoretically predicted ones. Specifically, we will collect data from published sources and web-based data banks on topography, evapotranspiration, rooting soil-moisture storage, saturated subsurface storage, precipitation, and stream flow for selected drainage basins. Eventually we will parameterize the models using data from basins that differ in geological substrate, climate (precipitation/evapotranspiration regime), and vegetation. In addition, a finite control volume approach is required to specify the topology and geometry of the networks and treat the fluid-mechanical principles in terms of the Strahler classification of stream order. An example is a mass balance equation for a link-based enumeration of channel networks (Gupta and Waymire, 1998a, b). The widely used treatment of conservation laws based on the stream continuum hypothesis is not applicable here, because we characterize river networks as discrete fractal-like structures.

Another component of the research will focus on the dynamics of landslides and resulting vegetation succession on steep forested slopes in the tropics. Like earthquakes, landslides are a critical phenomenon (Bak et al. 1988, Paczuski 1995). Strain builds up in the system and then is suddenly released when a patch of soil and vegetation slides free. Plants then colonize the newly created patch of bare soil and succession proceeds. Data from aerial photography and satellite imagery show that the frequency-magnitude distribution of landslides is a power function. We will build mechanistic models of landslides that incorporate soil and vegetation parameters and study how mountain slope, soil particle characteristics, and hydration state affect resistance to shear stress, vegetation mass interacts with gravity to create strain, and roots interact with soil properties to influence spatial connectance. A successional model will be used to predict vegetation change following a landslide. Together, the two models will predict the sizes, frequencies, and vegetation composition on the landscape.

c) Wagner and Fell: Universal design principles and scaling of metabolic networks

Networks of metabolic pathways are complex systems in themselves, but they also represent evolved mechanisms for deriving energy and other essential resources from the environment. Do large metabolic networks in different organisms share common design principles? Wagner and Fell will address this question with a comparative study of five well-studied unicellular organisms, assembling databases of all chemical reactions required for energy metabolism and synthesis of small molecules. A pilot study of *E. coli* demonstrated that this is feasible and revealed two previously unrecognized patterns (Wagner and Fell submitted). One pattern, shown by a graph-theoretical representation, is that core metabolism of *E. coli* belongs to a particular class known as small-world graphs. Small-world graphs have recently been characterized and found in such diverse structures as the *C. elegans* nervous systems and sociological friendship networks (Watts and Strogatz 1998). Such graphs are very sparse and highly clustered, so that most of the few connections between vertices (metabolites) are tied up in local interactions within cliques of metabolic pathways. Nevertheless, each vertex can be reached from any other vertex by a small number of steps, very close to the theoretical minimum number. The second pattern is that the distribution of connectivity in the *E. coli* metabolic network can be described by a power function.

Extending this analysis to other organisms will address the question of whether these two design features are ubiquitous. The study will compare four eubacteria and (*E. coli*, *Haemophilus influenzae*, *Heliobacter pylori*, *Bacillus subtilis*) and one eukaryote (*Saccharomyces cerevisiae*). These were chosen because: i) there is sufficient information on their biochemistry, genome, and general biology; and ii) they differ in phylogenetic relationships and life histories. Given the great variation in metabolic pathways across organisms, universal features of network design would suggest some combination of: i) selection to maximize rates and energy yields of pathways between metabolites (Watts and Strogatz 1998, Wagner and Fell submitted); and ii) historical phylogenetic constraints on the organization of the networks (Barabasi and Albert 1999, Wagner and Fell submitted).

d) Gosz, Li, Over, and Wu:

This group will focus on the dynamical basis for the fractal-like structures and processes observed in hierarchically self-organized populations, communities, and ecosystems. Examples of such phenomena include Taylor's power law of population fluctuations (op. cit.) and the distribution of vegetation patch sizes on the landscape (Milne 1998, Gosz et al. unpublished). We will explore these scaling relationships from mathematical, energetic, and thermodynamic perspectives.

Mathematically, we have demonstrated that interaction of simple elements on a microscopic level may result in the emergence of complex scaling features on a macroscopic level (Li et al., 2000), and that internal and external noise, multiplicative stochastic processes, and simply mixed distributions can cause scaling with power functions in ecological systems (Li et al., 1992; Li, 2000a,b). We have also used the space-time theory of multifractals (Over and Gupta, 1996) to investigate emergent properties of vegetation dynamics in space and over time (Over and Li, in preparation). These results were based on straightforward physical and biological principles and very limited assumptions; they reflected the outcomes of co-evolutionary or adaptive processes in which ecological entities such as populations or vegetation patches interact with their stochastic biotic and abiotic environment. Understanding the causes of scale invariance or covariance in space and time is important for interpreting such patterns as species-area and species-time

relationships. We have predicted scale breaks and cross-over properties in theoretical models of trophic dynamics in aquatic ecosystems (Li et al., in preparation), and demonstrated these phenomena in 10-year records of ecotone dynamics from vegetation transect data from the Sevilleta LTER (Over and Li, in preparation). In this proposal, we will continue to apply such mathematically and physically-based approaches to investigate the emergence of complex scaling at population, community, and ecosystem levels. We will focus on mechanisms that produce emergent spatial and temporal patterns in biodiversity by linking the dynamic scaling of structure and dynamics between populations and ecosystems. Such linkages should also make explicit connections with the allometric, life history, and landscape scaling relationships being studied by other groups.

We will study how emergent scaling properties of biodiversity with a macroscopic eigendynamics depend on the microscopic interactions with a microscopic eigendynamics. At the microscopic level, individual organisms interacting with each other and their abiotic microenvironment commonly create order parameters, which in turn feed back to affect the dynamics of communities and ecosystems, resulting in a circular causality (Li, 2000b). In addition, interactions evolve and change the environment, which in turn influences the further development, diversity, and stability of the system at both micro- and macroscopic levels. We will use nonlinear physics-based models that incorporate both thermodynamic constraints and biological strategies, as well as approaches from synergetics and autowave processes to search for general principles of self-organization of biodiversity. We will use Sevilleta LTER vegetation data and remote sensing imagery to detect multiple scale-related patterns and processes of biodiversity and to test predictions of the theoretical models.

e) Breshears, West, Brown: Extending scaling relationships to root networks of individual plants and plant communities

West, Brown, Enquist, and Charnov (Enquist et al. 1998, 1999, West 1997, 1999a,b) have modeled and tested scaling relationships for above-ground components of individual plants and plant communities. We will extend this approach to model below-ground root networks. We will evaluate and apply methods to characterize the fractal-like nature of root architecture, including different root growth forms (e.g., tap vs. fibrous). Implicit in this research is a theoretical and empirical comparison between the resource distribution networks of xylem in above-ground stems that have been studied to date (op. cit.) and the below-ground resource collection networks found in roots. Allocation of carbon, water, and nutrients among plant parts is an area of plant ecology in need of theoretical synthesis. We will begin to address this problem by characterizing the biophysical principles that underlie strategies of allocation over a wide range of conditions. Roots are also subject to different biomechanical constraints than above-ground structures, but they must take up water and soluble nutrients from a complex three-dimensional soil environment. We will start with the model for the above-ground distribution network, but modify or extend critical assumptions in three important ways: i) evaluate the biomechanical constraints of above-ground structure and the roots themselves on the branching rules for roots; ii) modify the above-ground model to account for growth and dieback of components of the root network; and iii) extend the theory to account for root architecture responses to amounts and heterogeneity in above-ground resources, such as CO₂, below-ground resources, such as water and N, and the effects of neighboring plants (e.g., Ehleringer et al. 1991, Brisson and Reynolds, 1994, Breshears et al. 1997, Pregitzer et al. 2000). This work will

provide a foundation for integrating the functional designs of roots and stems, for modeling the structure and dynamics of plant populations and communities in water- and nutrient-limited environments, and for better understanding the relationships of roots to soil properties, microbial symbionts, and other below-ground ecosystem components.

f) Waide and Willig: Body size, productivity, and species diversity

Spatial variation in species diversity is influenced by many factors; they include extrinsic environmental conditions, such as area, productivity, and physical heterogeneity, and intrinsic characteristics of the organisms, such as body size, trophic position, and taxonomic identity. Despite a growing literature on the relationship between species richness and three variables, area, productivity, and body size (e.g., Brown 1995, Rosenzweig 1995, Brown and Lomolino 1998, Waide et al. 1999, Gross et al. in press, Scheiner et al. in press), there has been little effort to reconcile these patterns. We will investigate these relationships using the data bases currently available or being compiled by NCEAS (Reichman et al. 1999) and the LTER sites. We hypothesize that species richness is scale-dependent with respect to the above three variables: i.e., not only does number of species vary with sample area, but the slopes and other diagnostic statistics of species-area relationships depend on both productivity and body size, with species being added more rapidly in productive than unproductive environments, and species of small size being added more rapidly than larger species. Additionally, relationships among these variables may exhibit discontinuities or scale breaks across habitats or biomes that differ in productivity or vegetation structure. Thus, for example, we expect to find differences in species-area relationships and distributions of body sizes within temperate grasslands and forests, and changes in scaling relationships across the boundaries (ecotones) separating these biomes.

g) Student research projects: listed below are some of the doctoral thesis projects that are directly related to this proposal :

1) Michael Fuller: Evolution of canalized epigenetic networks

Some developmental pathways are highly variable, whereas others are highly “canalized” or buffered against genetic and environmental changes. Models of transcription networks suggest that interactions among genes (i.e., epistasis) are mediated by gene products and play an important role in canalization (Wagner 1994, 1996). Does such canalization limit the evolutionary plasticity of epigenetic networks? Fuller’s thesis will address this question by: i) computer simulation models of the response of networks to genetic (mutation, recombination, and drift) or environmental changes (e.g., in metabolic substrates); and ii) selection experiments with the aerobic bacterium *Pseudomonas fluorescens*. In the latter, cultures will first be subjected to strong selection to induce canalization, and then: i) either kept under the same conditions (controls); ii) subjected to strong directional selection to assess rate of evolution to a new canalized state; or subjected to relaxation of selection to assess influence of drift and other spontaneous genetic changes. Previous work on *P. fluorescens* (Rainey and Travisano 1998, Rutherford and Lindquist 1998) shows that it is well suited for such experiments.

2) Ethan Decker: Scaling of cities

Investigations of global ecology must incorporate the effects of humans. Decker is studying ecological characteristics of cities and the ecological factors that influence them. Quantification of global urbanization and population distribution reveals that the size distribution of large cities follows a power function, but the distribution of smaller settlements may be lognormal. Data on fluxes of energy and materials and growth for cities of varying size will show whether these

relationships are allometric, and will be used to investigate the mechanisms. A simple model of urbanization that so far incorporates population growth, migration, and resource limitation is being used to explore the relationships between macroscopic patterns of population distribution and microscopic behavioral and demographic processes.

3) Ford Ballantyne: Unifying principles underlying Taylor's power law

The British ecologist L.R. Taylor (op. cit.) showed that the relationship between the variance and the mean for spatially dispersed populations of a species is well fit by a power function. Such a relationship could easily result from mixtures of lognormally distributed processes (Li et al. 1992, Allen et al. submitted, see proposed research of Gosz group above). The power functions fit to different species have different constants, Y_0 and b . The question is, what variables account for this variation? Can these variables be parameterized in a way that collapses the variation to a single power function with a universal exponent? Ballantyne, with a Master's Degree in mathematics, will explore the theoretical basis for Taylor's power law and evaluate the theory using the extensive data on population time series.

4) Andrew Allen: Self-organization of landscapes of microbiotic crusts

Microbiotic crusts offer an exceptional opportunity to use microcosms to experimentally test hypotheses about the role of energy and water in the formation and scaling behavior of "fluvial" landscapes. These crusts are assemblages of lichens, cyanobacteria, algae, mosses, and fungi that form small discrete patches on the soil surface in arid ecosystems. Measurements of the microtopographies of crusts at the scale of millimeters suggest that they exhibit the same scaling exponent (-0.45) as real fluvial topographies at the scale of kilometers, and the same as simulated terrain obtained via the principle of energy minimization (Rinaldo et al. 1992, Rodriguez-Iturbe and Rinaldo 1997). In controlled experiments, Allen will vary light and water supply, and monitor the changes in crust topography to test the hypotheses that the microbiotic crusts develop a landscape that either maximizes power or minimizes energy spent in transport.

5) Allen Hurlbert: Spatial scaling of biodiversity

How does diversity scale in space? Species-area relationships provide some insight, although the meaning of the exponents and specific mathematical form remain poorly understood (see above and Rosenzweig 1995, Harte and Kinzig 1997, Harte et al. 1999). Hurlbert is compiling and analyzing data on spatial patterns of diversity, using the Breeding Bird Survey and other data sources. He is also doing field research on local coexistence and spatial turnover of species of both hummingbirds and hummingbird-pollinated plants. The goal is increased understanding of the processes that affect the diversity of interacting species at scales from local communities to the entire North American continent.

6) Ethan White: Community dynamics in response to climate change

Recent analyses of data from Brown's Portal LTREB site and other sources suggest that while the abundances of individual species have shifted dramatically in response to recent abiotic environmental changes, certain emergent community-level properties, such as species richness and total abundance and biomass of all species, have remained essentially constant (Frost et al. 1998, Ernest and Brown submitted). One framework for analyzing community dynamics is the species-time relationship (Rosenzweig 1995). White will use the long-term time series of rodents and plants at Portal to assess the influences of sampling and environmental change on species-time relationships. Unmanipulated control plots and experimentally perturbed plots differ substantially in species composition, allowing assessment of whether species-time curves

have similar quantitative forms across different environmental conditions and taxa.

7) Drew Kerkhoff: Physical bases of plant canopy features

Kerkhoff is studying how physical processes constrain the structure and function of ecosystems, using piñon- juniper woodlands of New Mexico as a model system. He uses steady-state water balance models to predict an “ecologically optimal” distribution of tree canopies over a heterogeneous landscape. The idea is that changes in growth and reproduction of individual trees cause canopies to respond to water stress due to local climatic and hydrological conditions.

While the vegetation may lag behind short-term changes in the environmental driving variables, canopies should asymptotically approach the predicted ecohydrological equilibrium.

Components of the research program include: i) testing model predictions using high resolution remotely sensed tree canopy data; ii) evaluating alternative methods of space/time averaging; and iii) taking field measurements to estimate growth and reproductive responses to changing environmental conditions.

Timetable and Priorities

Our groups of collaborators have developed distinctive styles and schedules for working together. For example, Brown, West, Charnov, and Breshears work together intensively one day per week, usually at SFI. Milne and Gupta, having recently spent a sabbatical together, will now travel to each other’s institutions for extended visits of several weeks. A similar model will apply to the collaborations among Gosz, Li, Wu, and Over, Wagner and Fell, and Waide and Willig. To promote communication and synergy among these groups, we will hold an annual meeting where we will present, review, and critique each other’s work. To provide external review of our program, we will invite 2-3 scientists from outside our group to these annual meetings. To promote communication with other scientists with similar interests we plan to host workshops or symposia on approximately an annual basis, often in collaboration with SFI. Current plans call for two workshops: i) *Fractals in Biology* at SFI in fall 2000; and ii) *Emergent Structures and Dynamics of Networks* at Sevilleta in fall 2001. We expect some of these workshops/symposia to result in edited volumes, such as the SFI Symposium volume on *Scaling in Biology*. (Brown and West 2000).

To promote rigorous interdisciplinary graduate training we will structure the curriculum around the following requirements: 1) regular participation in the Ecological Complexity Seminar, which meets Wednesdays at 4:00; 2) enrollment in the SFI Complex Systems Summer School; 3) in addition to the graduate core curriculum of the Department of Biology, selection of at least two graduate-credit courses from other departments such as Mathematics, Physics, Computer Science, Earth and Planetary Science, Sociology, Anthropology, or the Certificate Program for High Performance Computing. In addition, students will be encouraged to collaborate with scientists or other students from outside of Biology, participate in the informal meetings of multiple lab groups, attend national meetings and present papers or posters, and conduct their research so that they can complete some projects and submit the results for publication well before finishing their degrees.

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MANAGEMENT PLAN

Every effort will be made to keep project management simple. We want to maximize the science, and minimize the management and administration. The “ecological complexity” group at UNM works because there is a solid core of about 20 faculty, postdocs, and graduate students who share common interests, enjoy interacting, and want to do collaborative science.

Lead institution: The University of New Mexico will be the lead institution. While the grant will support scientists from other institutions, they will be appointed as adjunct or research faculty so their salaries and expenses can be paid through UNM. This will avoid expensive and administratively cumbersome subcontracts to their home institutions. Continuation and enhancement of the vital relationship with SFI and LANL will also be handled without a subcontract. As with the current NSF GRT Grant, tuition to the SFI Complexity Summer School, commuting expenses for attending seminars, exchanging visiting scientists, and support for student interns will be paid out of the UNM budget.

Project manager: Despite our desire to minimize administration, we will require a part-time project manager. The Co-PI’s, Brown, Milne, and West, are active research scientists. They will assume responsibility for leadership and management of the project, but will need help with day-to-day coordination and oversight. We are confident that this can be done by recruiting a postdoctoral scientist with organizational talent and experience, and having him/her devote half-time to project management activities. This person will be responsible for maintaining the “complexity group” web page, coordinating the schedules of visitors, preparing announcements and reports of group activities, tracking performance and professional advancement of postdocs and students, and so on.

Bookkeeping, clerical, and secretarial tasks: Browns half-time assistant, paid by UNM, does these things for the GRT, and will do the same for the proposed project.

Promoting interaction and integration: The Co-PIs will assume primary responsibility for the conduct of the science. They share a common vision for keeping UNM at the forefront of developments in ecological complexity. We believe in the need to do rigorous, high-quality research, but also to be creative, unconventional, and risk-taking. Our experiences have taught us that the greatest rewards that can come from participating in interdisciplinary, collaborative science. We recognize the importance of walking the fine line between fostering innovation, creativity, and independence and promoting interaction, collaboration, and integration. With support from the GRT, we have established a successful model. It works well, but can be fine-tuned and improved. Investigators work on their own or more frequently in small groups, but they come together frequently to present their ideas and results, interact with visitors, and discuss recent literature. There are two primary vehicles to assist such integration: i) the Wednesday afternoon Ecological Complexity Seminar that is attended regularly by all graduate students and postdocs and by several faculty (especially Brown, Milne, and Li); and ii) the Ecological Complexity Web Page that is currently maintained by the GRT student trainees. It posts a wide variety of information, including essays and reading lists for seminars, schedules of visitors, and announcements of courses, meetings, and job advertisements.

EDUCATIONAL ACTIVITIES

The wording of this NSF Competition in Biocomplexity reflects recognition that a new kind of science is required to make substantial progress in understanding complex systems. The success of this endeavor will depend largely on the next generation of scientists - on how these new people are trained and on whether they can obtain jobs and research grants to apply their special knowledge and skills. We are training students and postdocs to fill these roles. In particular, graduate education provides much of the glue that bonds the “ecological complexity” group at UNM.

Development of our interdisciplinary graduate program has benefited enormously from a NSF Graduate Research Traineeship Grant, which unfortunately expires in 2001. The GRT provides support for 5 student fellows each year and makes possible many additional educational opportunities. Trainees with diverse backgrounds are recruited (they include undergraduate majors in English, sociology (2), anthropology, computer science (2), and environmental science, in addition to biology. Students are in different degree programs and they take individualized courses (Ph. D. Programs in Computer Science, Anthropology, and Sociology, M.S. Degrees in Mathematics and in Environmental Policy and Management; courses in physics, computer science, economics, and advanced mathematics). All are required to take the Wednesday Ecological Complexity Seminar and the SFI Complexity Summer School. More intangible activities are equally important. One example is the Ecological Complexity Web Page, maintained by the students. UNM generously agreed to return all administrative costs (overhead) to the GRT, and these funds provide a flexible basis for supporting many activities: bringing prospective students to UNM for interviews; sending students to scientific meetings, to SFI for seminars and workshops, and to other laboratories or investigators for additional training; bringing to UNM visiting scientists of all ages and stages, but including one distinguished Ecological Complexity Seminar Speaker per semester (past ones include ecologists C. S. Holling, E. P. Odum, and S. R. Carpenter; physicists M. Paczuski, P. Bak, and R. Sole; developmental biologists J.T. Bonner and S. Kaufman; and computer scientist J. Holland); providing additional support for student research projects, especially during the summer; and buying special books, computer hardware, software, and other supplies for joint student use.

The result has been the training of a new kind of ecologist. Student dissertation topics include artificial life, adaptive computer programs, human social systems, global human impacts, landscape distribution of endangered species, geographic patterns of biodiversity, biological allometry, and models of life history, population dynamics, community processes, and food webs. Students have published in *Science*, *Nature*, and the best specialty journals, been invited to participate in workshops and symposia, and been asked to write book chapters and *Annual Review* articles. While the GRT is currently in its fourth year and most of the trainees have not yet completed their degrees, those that have finished have readily obtained prestigious postdocs (e.g., three at NCEAS and two at SFI) or high-paying jobs in the biotech industry (National Center for Genome Resources).

We want to continue to train these kinds of scientists. Consequently, a large proportion of this proposal is devoted to educational activities. Specifically, we will maintain and strengthen four components of our educational program:

i) recruiting and training graduate students:

The budget includes stipends for 7 Research Assistants (RAs). These assistantships will be used

to recruit Ph. D. students with diverse backgrounds and exceptional promise. Because we are acquiring a reputation as an unconventional, exciting place for young people to do new kinds of ecology, we get outstanding graduate applicants. But we need to offer financial incentives to encourage students to come to UNM (instead of larger, wealthier institutions) and to support them while they are here. The RAs will serve the role of the current GRT Traineeships. They will be allocated to some combination of new and continuing Ph. D. students in order to recruit them into the program and to support them as they take special classes and do unusual research projects. RAs will be closely supervised by a major advisor and dissertation committee, but they will be encouraged to be independent, to obtain unique kinds of interdisciplinary training, and to develop interdisciplinary collaborations across and beyond the UNM campus. They will be required to take a “core curriculum” that includes the SFI Complexity Summer School and regular participation in the Wednesday Ecological Complexity Seminar.

ii) postdoctoral positions: We have been fortunate to have postdocs (Brian Enquist, Carla Restrepo, and Madur Anand), who have been supported on fellowships or faculty research grants but who have participated regularly and enthusiastically in the “ecological complexity” group. These postdocs are receiving a special kind of research experience at UNM, but they are also making an enormous contribution to training graduate students. They often take the lead in initiating collaborations that bring together students with different advisors and interests. We request support for three postdocs (one of whom will be the half-time project manager). These postdocs will be recruited to bring special backgrounds and dimensions to the group. They will have a faculty advisor, but will be expected to exercise considerable independence in developing research projects and collaborations.

iii) undergraduate students: We have had spectacular but limited success in involving undergraduates in ecological complexity research. This is unfortunate, because UNM has some outstanding undergraduates, including a high proportion of minorities and other disadvantaged groups. Most undergrads are juniors or seniors before they settle on an ecology track major and start taking advanced courses where complexity is mentioned. A few, however, do get their interests piqued, become involved in research, and have their lives changed forever. For example, John Haskell, has been working for about a year in the Brown lab, is an undergraduate intern for the NCEAS Body Size Working Group, will probably be author of at least four papers before he graduates in December, and then plans to do Ph. D. research at Utah State with Mark Ritchie. We have concluded that ecological complexity is likely to appeal to only a few select undergraduates, but we make every effort to attract, encourage, and support those who show a genuine interest.

iv) collaborative training with SFI: The GRT Trainees are unanimous that taking the SFI Complexity Summer School and participating in other SFI activities is an invaluable experience. In addition to the course, students are able to attend seminars and interact one-on-one with the distinguished scientists from many different fields who visit SFI. SFI typically has at least one workshop each year devoted to some ecological topic, and 4 or 5 UNM grad students serve as assistants to these workshops, benefiting enormously not only from hearing the presentations and discussions, but also from the opportunity to talk individually with the scientists. Two Ph. D. students from the UNM “ecological complexity” group, Timothy Keitt and Brian Enquist, have gone on to become extremely successful postdocs at SFI. There is strong interest from both parties to maintain and strengthen the UNM-SFI connection.

JUSTIFICATION OF BUDGET

Note: the following explanation is based on the first-year budget. Except for equipment, budgets are increased 5% per year.

A. Senior personnel:

The ½ to 1 month of summer salary per year will be allocated to senior scientists based on a combination of need and performance.

B. Other personnel:

- 1) Postdoctoral associates: We ask for three postdocs per year. We will advertise, solicit applications, select candidates, and assign postdocs to mentors and collaborative groups based on interests and merit. As mentioned in the proposal, one postdoc will be expected to allocate 50% of his/her time to serving as Project Manager; duties are described in the management plan.
- 2) Other professionals: We ask for a half-time computer network administrator. The Department of Biology is expecting to pay the other 50% of his/her salary. We know from experience that the “complexity group” needs at least a half-time person to service and update software and hardware.
- 3) Graduate students: We ask for 7 graduate research assistants per year. Experience with the GRT indicates that we attract outstanding student applicants. Students will apply for the assistantships during a posted application period each year. Selection of research assistants will be based on a combination of need and merit.

C. Fringe benefits: Rates: 24% for senior personnel and other professionals, 14% for postdoctoral associates, and 1% for students.

D. Equipment: We request 2 workstations @ \$10,000 each and two desktop computers @ \$2,500 for the first year, and two desktop computers per year thereafter. This regime would replace most of the existing machines used by the “complexity group” on a 3-5 year cycle.

E. Travel:

- 1) Domestic: Based on: i) 15 scientific meetings per year @ \$1,100 per meeting for senior scientists, postdocs, and graduate students; and 4 visits per year of senior scientists to collaborators’ home institutions @ \$3,250 per visit (\$750 for air fare and 33 days @ \$75 per diem).
- 2) Foreign: Based on two visits per year of senior scientists to collaborators’ home institutions overseas @ \$3,500 per visit (\$1,000 for air fare and 33 days @ \$75 per diem).

F. Participant support: None, all charged as travel.

G. Other direct costs: Very modest amounts are requested for:

- 1) office expenses (supplies, photocopying, etc.)
- 2) publication costs (page charges and reprints)
- 3) computer services (for site licenses, repair, and service)
- 4) other: this includes annual amounts of \$19,600 for tuition for graduate research assistants, \$3,000 for teleconferencing facilities to support long-distance collaborations, and \$10,000 for purchase of software

SPECIAL INFORMATION

Letters of agreement from SFI and LANL