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Ecological Research Division

THEORETICAL ECOLOGY PROGRAM

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PREFACE

The Department of Energy (DOE) and its predecessors have supported research in terrestrial ecology for more than 30 years. The ecology program evolved in the 1950's out of a need to know the transport and fate of fallout radionuclides and possible pathways from the ecosystem to humans. Even though radionuclides posed an environmental problem, they provided an excellent tool for investigating processes through entire ecosystems and for measuring process rates within ecosystems. With this tool, quantitative ecology developed dramatically in the 1960's, revolutionizing the entire field. At the same time, quantitative ecology highlighted the need for rigorous theory in this newly emerging science. Thus over the years, the DOE terrestrial ecology program provided a small amount of funding to support theory development.

Recent attention to global change has highlighted the requirement for a much better understanding of terrestrial ecology and its role, not only in climate change, but also in desertification, soil deterioration, and contaminant transport. Expansion of theory development was urgently needed, for these reasons and to provide a better focus for ecological research. As a result, in 1988 the Ecological Research Division began a program devoted to theoretical ecology, issuing the first solicitation for proposals late that year. Because resources came out of the existing funding base, the budget for the solicitation was necessarily limited. Out of the 60 proposals submitted, 8 were awarded funds in the first year and 2 the next.

This report presents the goals of the Theoretical Ecology Program and abstracts of research in progress. Abstracts cover both theoretical research that began as part of the terrestrial ecology core program and new projects funded by the theoretical program begun in 1988. Projects have been clustered into four major categories:

- Ecosystem dynamics.
- Landscape/scaling dynamics.
- Population dynamics.
- Experiment/sample design.

Our objective is to maintain a strong Theoretical Ecology Program and ensure a constant infusion of new ideas by issuing an open solicitation for proposals every 1 to 2 years. Plans also include a major information meeting at least every 3 years to review progress of the program and explore additional directions. Information about program status and planned proposal solicitations can be obtained by contacting the program manager at the following address:

Program Manager for Theoretical Ecology
Ecological Research Division, ER-75
Department of Energy
Washington, D.C. 20545
Telephone (301) 353-4208
FAX (301) 353-5051

In closing I would like to thank the people who have managed the Theoretical Ecology Program. They came to DOE for 1- to 2-year assignments and brought a fresh perspective to terrestrial ecology research at DOE. Dr. Edward Rykiel, Texas A&M University, initiated the Theoretical Ecology Program and developed the first solicitation for proposals. Dr. Walter Conley, New Mexico State University, organized and ran the panels to review the proposals. Dr. Clive Jorgensen, Brigham Young University, presently manages this program and has prepared most of the material in this document after discussions with the principal investigators. The Ecological Research Division and the Theoretical Ecology Program have benefited greatly from the enthusiasm and dedication these three scientists have devoted to the development and implementation of the program.

Helen M. McCammon, Ph.D.
Director, Ecological Research Division, ER-75
Office of Energy Research

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THEORETICAL ECOLOGY PROGRAM

Introduction

In 1988, DOE's Ecological Research Division initiated a new program for the express purpose of fostering the development of ecological theory. Theory is often neglected in research funding, and this program is the first devoted specifically to the support of theoretical ecology. Much earlier, DOE pioneered the development of modeling and systems analysis in ecology, and the Department and its predecessors are well known in the scientific community today for contributions to theory in many areas of ecology. Therefore, DOE and the Ecological Research Division are especially sensitive to the need for theoretical developments to guide leading ecological programs.

The Theoretical Ecology Program is now supporting a variety of studies with funding of approximately $2 million. Although small in funding terms, it is the only program focused primarily on seeking fundamental theoretical advances in ecological and environmental sciences. Because theoretical advances often emerge from unpredictable beginnings, goals of the program are stated broadly, as follows:

(1) To provide the fundamental theoretical basis needed to understand complex ecological systems.

(2) To predict the behavior of such systems at all scales of resolution and organization.

(3) To guide data collection and analysis.

(4) To identify the most significant directions for future research.

Rationale

Theoretical research must meet DOE needs, but it must also be directed to state-of-the-art research. As such, it must contribute to the development of new unifying theory, significantly advance current ecological theory, and/or explore new approaches, methodologies, and paradigms (see figure 1). Presently, program interests include, but are not limited to, integrating processes across multiple levels of ecological organization with special reference to global change, scaling the analysis of ecological structure and function, and analyzing spatial and temporal dynamics of nonlinear environmental systems. Interdisciplinary research that includes collaboration with other disciplines such as physics, meteorology, and earth science is particularly encouraged. The immense value of integrating experimental research with theoretical development is well recognized. However, the current level of funding requires a sharp focus on theory and therefore may not permit extensive independent laboratory and field experiments. Investigators are encouraged to use data from ongoing DOE-sponsored research and the DOE National Environmental Research Parks whenever possible.

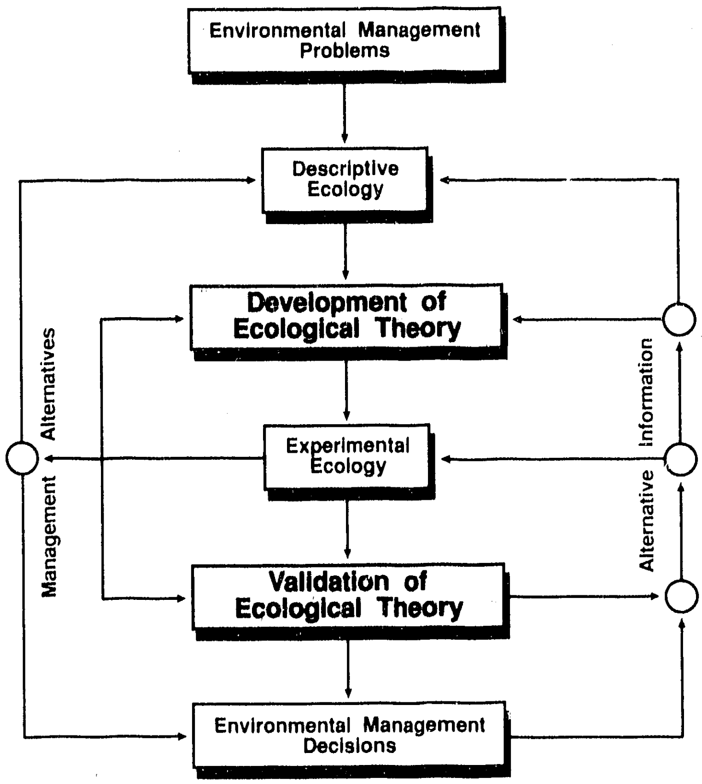

Figure 1. Flow diagram to illustrate the integration of Theoretical Ecology with Descriptive and Experimental Ecology.

Ecological problems important to DOE are environmental concerns related to energy development and use: air quality, waste management, ecological remediation, water quality, biodiversity, biomass production, global climate changes, and energy resource extraction. Once these and other problems are defined as environmental management concerns, research can be designed to facilitate reasonable management decisions. Although management decisions often rely only on descriptive data, well-validated theory provides a foundation for better decisions.

All proposals submitted for DOE's review should clearly present the appropriate research alternatives or combinations of alternatives (descriptive, experimental, and theoretical). This procedure should demonstrate how the research proposals described (1) contribute to existing ecological theory, (2) meet the needs for new theory and/or different forms of data, and (3) disagree with existing theory.

Funding in the Theoretical Ecology Program

For fiscal year 1990, funding for the Theoretical Ecology Program is $2.179 million out of a total of $8.122 million for all terrestrial ecology research. For many years, until 1988, support for theoretical ecology was approximately 13 percent of the ecology budget. In 1989, it increased to 22 percent and, in 1990, rose to 27 percent of the total budget. Figure 2 illustrates this upward trend. The decrease in the overall budget from 1989 to 1990 was due to the sequester of 1.4 percent required by the Gramm-Rudman-Hollings deficit reduction bill. About 75 percent of the funding in theoretical ecology goes to universities, the rest to DOE's National Laboratories.

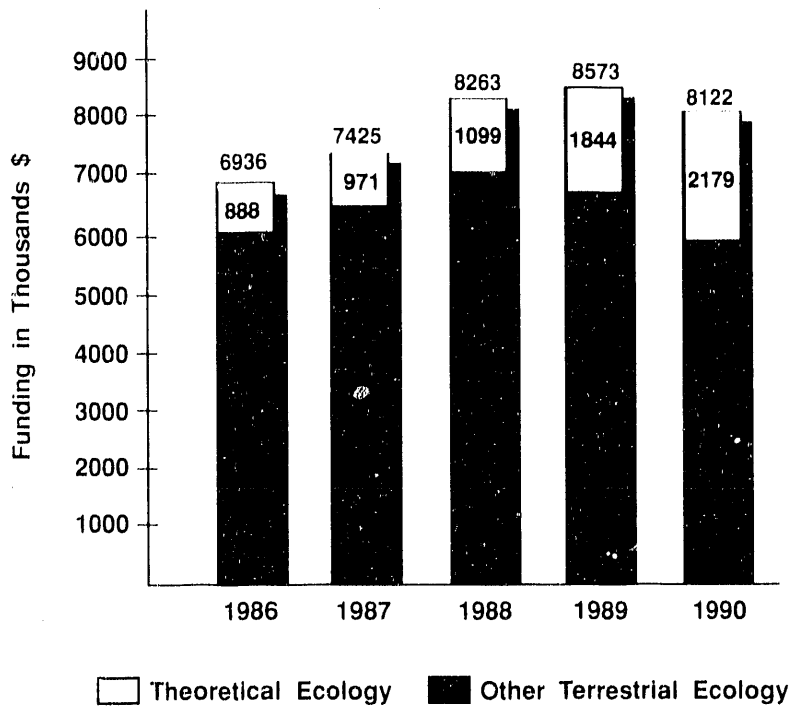

Figure 2. Funding levels in the Terrestrial Ecology and Theoretical Ecology Programs.

Management of the Theoretical Ecology Program

Within DOE, the Theoretical Ecology Program is sponsored by the Ecological Research Division of the Office of Health and Environmental Research. The program is managed by university researchers who spend 1 to 2 years in the Division. The following people have served as program managers and have developed and implemented the terrestrial ecology program:

- Edward J. Rykiel, Texas A&M University, developed the program plan and convinced DOE management of the program's extreme importance. In 1988, he formulated the public announcement inviting proposals for funding.
- Walter H. Conley, New Mexico State University, selected, organized, and ran the panels reviewing the proposals in 1989. Of the 60 proposals submitted, 10 were ultimately funded.
- Clive D. Jorgensen, Brigham Young University, has compiled this report. He will organize a major meeting and a review of the Theoretical Ecology Program in the next year.

The goal of the Theoretical Ecology Program is to issue one open solicitation a year for new proposals. If budget constraints are unavoidable, an open solicitation will be held at least every other year. Public announcements are usually made in the *Federal Register*. Information about status of these public announcements can be obtained from the program manager of the Theoretical Ecology Program, whose address and telephone number appear in the preface.

New proposals are sent for outside peer review whether they are submitted as a result of public announcement or as unsolicited proposals. A panel of peer reviewers evaluates proposals that respond to public announcements. Unsolicited proposals are reviewed by mail and then evaluated internally; they compete for funds from the terrestrial ecology core program.

All projects in the Theoretical Ecology Program are reviewed every 3 years, including those that originated as part of the terrestrial ecology core program. Renewal for another 3 years is contingent upon progress of the research, the scientific and technical merit of the project, and the likelihood of the research leading to significant advances in the field.

The abstracts in this report include no theoretical or modeling projects that are an integral part of watershed projects being carried out at the Oak Ridge Walker Branch Watershed or the DOE Arctic R4D site. Nor do the abstracts describe largely experimental projects that include some theory or modeling. Such integrated projects are covered in separate descriptions of terrestrial research sponsored by the Ecological Research Division. The terrestrial ecology core research focuses on two programs, one devoted to development of and monitoring within an interactive network among the seven DOE National Environmental Research Parks and the other to multidisciplinary research focused on ecosystem structure and function in the watershed and landscape program.

The abstracts in this report are subdivided into four categories:

- Ecosystem dynamics—Productivity, habitat changes, and community dynamics.
- Landscape/scaling dynamics—Scaling concepts related to ecosystem processes and patterns over broad regions.
- Population dynamics—Population studies of plant, animal, and microbial systems.
- Experiment/sample design—Statistical approaches to developing optimum and cost-effective sampling programs.

These categories overlap somewhat, but the groups highlight the main emphases of the program. Each of the abstracts also describes the relevance of the research to ecology and to the Department of Energy.

ECOSYSTEM DYNAMICS

Project Title

Theoretical Models of the Impact Climate Change Has on Natural Populations, Communities, and Ecosystems

Principal Investigator

H. Ronald Pulliam

Research Institution

Institute of Ecology
University of Georgia
Athens, Georgia 30602
(404) 542-6010

Research Description

Global and regional changes caused by anthropogenic activities will result in habitat changes and major shifts in the ranges and survival of the species. This research is developing theoretical models that will predict such species changes. One class of models focuses on temporal viability in climatically relevant environmental variables, the influence of these variables on population and community dynamics, and the evolution of life-history characteristics. Another class of models focuses on spatial heterogeneity and habitat-specific demographic changes. Three separate classes of temporal patterns in habitat heterogeneity will be considered: Class I, in which the spatial pattern is unchanging; Class II, in which the pattern changes continuously with time; and Class III, in which the pattern change is discontinued. Finally, selected models will be tested against empirical field data situations drawn from ongoing research.

Relevance of Research

Climate warming may induce enormous changes in plant and animal communities for some regions of the Earth. Environmental policy should rely on predictions about the magnitude and direction of these ecological changes. Constructing accurate comprehensive models for each kind of community would be an extraordinarily large task. Instead, this research is developing models for communities that exemplify important kinds of environmental variation. From the behaviors of these models, generalizations to guide predictions about ecological change in other analagous systems will be developed.

Project Title The Evolution of Functionally Organized Communities: Theory and Test

Principal Investigator David S. Wilson

Research Institution
Research Foundation
State University of New York at Binghamton
Binghamton, New York 13901
(607) 777-4393

Research Description

Theoretical models that explore complex interactions among species and genotypes within species in spatially structured populations are being constructed. As separate subjects, complex interactions and spatial heterogeneity have numerous important implications for ecology and evolution. Integrated together, they have additional implications that would be difficult to predict from either one alone. Two central foci are—

- Global species diversity—The joint effect of complex interactions and population structure can greatly increase the number of species that coexist globally.
- Functionally organized communities—Complex interactions can increase variation among patches in a metacommunity, which serves as the raw material for natural selection operating at the patch level.

Relevance of Research

At least three different paradigms of ecosystem organization exist among ecologists. The first largely ignores the fact that properties of species have been shaped by evolution. The second assumes that evolution produces well-adapted individuals who then interact in ways that do not necessarily produce well-adapted communities and ecosystems. The third assumes that evolution produces communities and ecosystems that are well adapted to their environments just as their individuals are. Each paradigm leads to a different vision of nature, with important consequences for management decisions. This project explores the validity of these paradigms and, therefore, contributes to our fundamental understanding of nature. It also has the potential to make practical suggestions for ecosystem management.

Project Title Environmental Productivity Indices and Productivity for Desert CAM Plants

Principal Investigator Park S. Nobel

Research Institution Department of Biology
Laboratory of Biomedical and Environmental Sciences
University of California, Los Angeles
Los Angeles, California 90024
(213) 825-3395

Research Description Indices ranging from zero to unity have been devised to quantify influences of environmental factors on the net CO_2 uptake, and hence productivity, of various crassulacean acid metabolism (CAM) succulents from arid and semiarid regions. These indices include a Water Index, a Temperature Index, and a Photosynthetically Active Radiation (PAR) Index. Based on the effects of water status, temperature, and PAR on net CO_2 uptake measured over 24-hour periods in the laboratory, they can be determined daily using values of the appropriate environmental parameters at a particular field site. The product of these three indices, the Environmental Productivity Index (EPI), then indicates the relative CO_2 uptake ability under a particular set of environmental conditions. A Nutrient Index, similarly ranging from 0.00 to 1.00, has also been proposed to quantify the influence of soil element levels on shoot CO_2 uptake. Using EPI, the productivity of various agaves and cacti has been predicted over wide geographical areas. For instance, productivity for *Opuntiaficus ficus-indica* has been predicted for 253 regions within 60° of the Equator using data from 1,464 weather stations. For a canopy of closely spaced plants, predicted productivities were at least 10 metric tons (dry weight) hectare^{-1} year^{-1} for nearly half of the Earth's land area. EPI and the measured response of CAM plants to elevated CO_2 levels can also be used to predict the productivity of *O. ficus-indica* on a worldwide basis for rainfall patterns, temperature changes, and PAR conditions, such as various manmade environmental changes that are predicted for the future.

Relevance of Research An Environmental Productivity Index can predict productivity of some plants for any region with available weather data. Also, predictions can be made for future or hypothetical climates, such as those projected to accompany a potential doubling in atmospheric CO_2 levels. Productivities for agaves and cacti have already been shown to exceed 20 metric tons (dry weight) per hectare per year, which exceeds the annual productivities of most conventional agronomic crops and hence has important implications for future land-use scenarios.

LANDSCAPE /SCALING DYNAMICS

Project Title

Spatial Scaling: Its Analysis and Effects on Animal Movements in Semiarid Landscape Mosaics

Principal Investigators

Bruce T. Milne[1] and John A. Wiens[2]

Research Institutions

[1]Department of Biology
University of New Mexico
Albuquerque, New Mexico 08101
(505) 277-3411

[2]Department of Biology
Colorado State University
Fort Collins, Colorado 80523
(303) 491-0985

Research Description

This project addresses two general questions:

- Are landscape patterns repetitive over different spatial scales?
- How does the patch structure of a landscape mosaic affect ecosystem dynamics and functions?

The first question is examined by determining the spatial distribution of patches at nested scales ranging from about 1 m^2 to 10 km^2. Fractal geometry and other tools are used to determine the domains of scale over which landscape patterns are scale independent. To answer the second question, movements of biotic vectors (ants and beetles) at several scales will be recorded and then related to the mosaic patterns and boundary configurations of microlandscapes. Experimental manipulations of landscape structure will be used to determine how such organisms may function in the redistribution of materials in patchy landscape mosaics. Together, these studies will be used in conjunction with computer simulation models of animal movements in spatial mosaics to develop new analytical approaches and concepts related to landscape patterns at many spatial scales.

Relevance of Research

The research on scaling will help to define the range of scales within which findings from field research can be extrapolated. These ranges may correspond to those over which the linkages between patterns and the processes that cause them are relatively stable. Defining such domains of scale is essential in comparing the results of studies conducted at different scales, because such comparisons will be valid only if the studies lie within the same pattern-process domain. The studies of vector movements will provide an operational protocol for addressing problems involving movements in heterogeneous landscapes at a variety of scales in many types of ecosystems. Linking movement of organisms to the landscape areas they occupy over a broad range of scales will allow development of theory that can provide the foundation for research in many areas of landscape ecology, epidemiology, material flows in systems, and animal behavior.

Project Title | Grassland/Atmosphere Response to Climate Change: Coupling Regional and Local Scales

Principal Investigators

Michael B. Coughenour and Timothy G.F. Kittel

Research Institution

Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523
(303) 491-5572

Research Description

Predicting the impacts of global changes in climate and elevated CO_2 levels on ecosystem processes is the task facing ecologists. This problem requires an understanding of the interactions among atmospheric and ecological processes operating at different scales. This research addresses the problem with a hierarchical modeling approach. It uses a regional and mesoscale atmospheric model to interpret global circulation model results at regional and finer scales. A protocol is being developed that uses physiological and soil process models to simulate multilevel and multiscale ecological response to CO_2 and climate change for hierarchical information exchange between high and low temporal resolution. Finally, these models will be used in a set of modeling experiments that demonstrate their utility in predicting ecosystem and atmospheric impacts of climate and CO_2 changes at multiple spatial and temporal scales for the North Americ n central grasslands.

Relevance of Research

Climate is the principal driving force that changes structure, function, and productivity of terrestrial ecosystems. Natural climate changes are inevitable, and manmade climate changes may be induced by fossil fuel combustion. The ability to predict ecological responses to these climatic changes is important for effective planning and policy development. However, ecological responses in local areas, such as individual ranches, farms, parks, etc., cannot be predicted accurately from regional or global scale analyses because larger scale analyses must necessarily be coarser, sacrificing the detail needed for a broader analysis. Similarly, analyses for short time periods (1 to 10 yr) are not easy to translate into predictions over much longer periods (50 to 500 yr). This project is seeking ways to ensure that predictions made at different spatial and temporal scales are consistent. This consistency will greatly improve ecological assessments of global-scale climate change scenarios.

Project Title A Theory of Forest Dynamics: Spatially Explicit Models and Issues of Scale

Principal Investigators Stephen W. Pacala[1] and Simon A. Levin[2]

Research Institutions

[1]Ecology and Evolutionary
Biology Department
University of Connecticut
Storrs, Connecticut 06268
(203) 486-2982

[2]Ecology and Systematics
Cornell University
Ithaca, New York 14853-2701
(607) 255-4617

Research Description

This research is empirically calibrating and testing a theory of forest dynamics that encompasses a broad range of spatial and temporal scales. The research consists of an integrated program of computer and mathematical modeling together with empirical studies of 12 forest tree species that are canopy dominants in transitional oak-northern hardwoods forests. The empirical studies provide the data necessary to explicitly calibrate spatial models of forested landscapes that include the following characteristics: (1) competition for light, water, and mineral nutrients; (2) dispersal; (3) disturbance; (4) soil and topographic heterogeneity; and (5) patterns of forest fragmentation. The models should be applicable to landscapes as large as 10^4 to 10^5 km^2 and yet should retain fine-scale resolution important to single individuals. The models are designed so they can be tailored to forecast the consequences of energy-related and other anthropogenic perturbations such as acid rain, elevated CO_2 and ultraviolet radiation, and global warming.

Relevance of Research

This research is designed to answer fundamental questions about the relationships of scale, pattern, and process in forest communities. These questions are relevant to an understanding of virtually any ecological system. In addition, the proposed work will produce models and methodologies of applied value. The forest communities studied cover extensive regions of eastern North America and are increasingly affected by energy-related and other perturbations, including acid rain, elevated CO_2 and ultraviolet radiation, and global warming. The models are designed so that they may be tailored to forecast the consequences of anthropogenic perturbations. A tailored model will also allow the identification of species and scales that provide the most useful indicators of whole-system response to atmospheric changes.

Project Title

Testing the Scale-Dependence of Models of Resource Competition and Environmental Conditions for Forest Structure and Dynamics

Principal Investigators

Robert G. Knox[1] and Paul A. Harcombe[2]

Research Institution

Ecology Department
Rice University
Houston, Texas 77251
[1](713) 527-4924
[2](713) 527-8101 ext. 2664

Research Description

This research is evaluating two models of forest community structure and dynamics previously developed at different spatial and temporal scales. Gradient models describe species distributions and community composition in terms of environmental factors, which can usually be associated with specified conditions for plant growth. Resource competition models explain community dynamics and resulting composition in terms of the acquisition of limiting resources. Recent developments in resource competition theory (extending explanation to large-scale gradients) and in analysis of small-scale variation in the growing environments make it increasingly clear that the potential scales of explanation for these two models are not mutually exclusive. Methods are being developed to make predictions using both approaches at scales where detailed data on forest composition and dynamics are available. Prospects for a synthesis of these two approaches are good. Nevertheless, an essential part of determining the limits of each approach is discovering areas where the models make different predictions and then evaluating these differences in light of field data. This research is testing regional gradient models and resource competition models for sets of intensive study sites representing major forest types on the coastal plain and piedmont of the southeastern United States. Because some key predictions of each approach cannot be readily made by others, empirical models of within-site spatial and temporal distribution (i.e., local gradient and stage projection models) will also be used to help test model limits.

Relevance of Research

A deeper understanding of the mechanisms controlling forest composition has the potential to contribute information relevant to a variety of policy and resource management issues. Forest response to global climate change may depend on identity and effects of the resources that limit production. Biogeographic constraints may also limit forest recovery following regional changes. Work toward a synthesis of empirical gradient models and mechanistic resource competition models will contribute to an understanding of these constraints. A synthetic theory of forest composition and production could also be relevant to future use of forests for carbon storage and renewable fuels.

Project Title

Simulation of Landscape Disturbances and the Effect of Climatic Change

Principal Investigator

William L. Baker

Research Institution

Department of Geography and Recreation
University of Wyoming
Laramie, Wyoming 82071
(307) 766-3311

Research Description

Natural disturbances periodically alter the landscape structure of many ecosystems, yet little is known about how global climatic change may affect landscape structure through changes in disturbance regimes. This research is developing a theoretical understanding of the relationships of atmospheric variation and variation in landscape structure in disturbance-mediated ecosystems. Three specific theoretical questions are being addressed:

- What is the effect of spatial heterogeneity on the spread of disturbances?
- Given a variety of disturbance regimes, what is the expected temporal variation in landscape structure, and how will this variation be affected by changes in climate?
- What is the effect of spatial and temporal sampling scales on the detection of stability or instability in landscape structure?

These questions are being addressed using simulation modeling followed by field testing. Initially, the model will be general, but it will be subsequently tailored for use in temperate-zone terrestrial forests disturbed by fire and in riparian forests disturbed by floods. Field data will be collected from three sites: (1) Animas River, Colorado, riparian forest site; (2) an Alaskan riparian forest site; and (3) an Alaskan forest disturbed by fire. Published historical data on the sizes and locations of fires since the 1960's in the Boundary Waters Canoe Area, Minnesota, and in Jasper National Park, Canada, will also be used.

Relevance of Research

The objective of this research is to develop understanding of the functional relationships between global atmospheric and climate change phenomena and the composition and structure of ecological systems (landscape structure). Particular attention is given to how the size and shape of disturbances (e.g., fires and floods) and environmental heterogeneity can be related (scaled) to larger ecological systems such as the landscape structure. For many communities that are periodically disturbed, the direct effects of increased atmospheric CO_2 levels may be masked by significant alterations in composition and structure resulting from changes in the disturbance regimes. This research addresses the problem of understanding how landscape structure changes under the influence of exogenous forcing functions (atmospheric and climate changes) and endogenous resistance functions (landscape composition and structure).

Project Title Systems Processes in Landscape Ecology

Principal Investigators Robert H. Gardner, Robert V. O'Neill, and Monica G. Turner

Research Institution

Environmental Sciences Division
Oak Ridge National Laboratory
Martin Marietta Energy Systems, Inc.
Oak Ridge, Tennessee 37830-6036
(615) 574-8282

Research Description

Ecological processes (e.g., disturbance/recovery, territoriality, and competition) interact with abiotic spatial factors (e.g., topography and soils) to produce spatially complex biotic patterns on the landscape. These patterns impose limits on the biota by determining suitable habitat and resources. The biotic interactions, in turn, alter these patterns by consuming resources and altering rates of recovery. This interplay between pattern and process forms a key subject for ecology in general and landscape ecology in particular.

This project is currently exploring theoretical approaches for integrating pattern and processes at various spatial and temporal scales. The use of percolation theory is being expanded by the development of models that include complex patterns generated by gradients and hierarchically structured landscapes. New work is under way to use epidemiology theory as an alternate model for the spread of disturbance across the landscape. Finally, models based on diffusion-reaction equations and patch dynamics theory will be used to determine potential interactions between ecological processes and spatial heterogeneity in the environment.

A package of analytical techniques for detecting pattern and scale in spatial data will be developed and used to compare model predictions with the extensive data bases available. In addition, data available from DOE's ParkNet and National Science Foundation's LTER sites will be used to test these results. Finally, efforts to develop simple descriptors of landscape pattern will continue with the exploration of texture indices developed in the field of image processing.

Relevance of Research

Over the past two decades, it has become abundantly clear that energy extraction and utilization affect the environment at regional (acid precipitation) and global (CO_2) scales. Although the need to understand broad-scale ecological pattern and process is urgent, ecology and other environmental sciences are relatively unprepared to address these major problems. Broad energy-related questions require regional-scale approaches that cannot be addressed by traditional site-specific studies. Emergent properties involve spatial heterogeneity and the patterning of ecological systems (e.g., vegetation) on the landscape. Spatial patterns relate directly to environmental quality and stability of ecological systems and may be altered by energy development and use.

These approaches to this critical area will combine mathematical theory, simulation modeling, and synthesis of existing data to test and apply theory. Sets of parameters that can be used to quantify these broad-scale patterns have been identified. These parameters will now be used in models designed to estimate landscape pattern change. A suite of models and scales of landscape resolution will be used to study how changes in the patterning of ecological systems affect ecological function.

POPULATION DYNAMICS

Project Title

Development of Paradigms for the Dynamics of Structured Populations

Principal Investigator

Alan M. Hastings

Research Institution

Division of Environmental Studies
University of California
Davis, California 95616
(916) 752-8116

Research Description

Lotka-Volterra equations have served as the basic paradigm in ecological modeling for many years. These equations, and the models based on them, were responsible for the embodiment of ideas such as the competitive exclusion principle and, even quite recently, those concerning the dynamics of food webs. However, as researchers have long recognized, these models represent a simplification of ecological reality. In particular, they ignore the consequences of structure within the populations modeled (i.e., spatial structure, age structure, physiological structure, genetic or phenotypic structure, and/or possibly others). This research is developing further theoretical understanding of the structured single-species and multispecies systems. It uses models based on systems of first-order partial differential equations, known as the McKendrick or vonFoerster equations. In particular, it is examining two kinds of structure within populations. First, the dynamics of interacting age or physiologically structured populations are being examined. The goal of this work is to determine what general properties emerge or, in examples where no general properties emerge, to determine at what level generalities do exist. Second, the dynamics of interacting spatially structured populations will be examined using the above modeling approach.

Within these general areas, the following specific questions will be asked:

- Can local "outbreaks" of pests be explained by predator-prey systems in "patchy environments"?
- What role do local dynamics play in the interaction between a predator and a patchily distributed prey?
- What are the patterns produced by competition in a patchy environment?
- Can the pattern produced be used to infer the presence of competition?

Relevance of Research

The importance of spatial and age structures to understanding the dynamics of natural populations has become accepted during the last decade. However, models have not been extensively studied that consider a metapopulation broken up into a series of subpopulations and that also explicitly include both numbers within patches and the effects of stochasticity on local population dynamics. These models, which are the primary focus of this research, are vital for understanding questions in conservation biology related to persistence of species. They are also vital to understanding the mechanisms and predicting the success of biological control. Finally, such models are also vital to understanding the process of competition in spatially structured systems.

Project Title Development and Testing of Theories of Population Dynamics

Principal Investigator William D. Murdoch

Research Institution Department of Biological Sciences
University of California
Santa Barbara, California 93106
(805) 961-2808

Research Description This research consists of several related projects, all aimed at developing testable models of the dynamics of populations of organisms. Models are being developed for the interactions between a zooplankter (*Daphnia*) and its algal food organisms; for a freshwater predatory bug (*Notonecta*); for giant marine kelp; and for the interactions between red scale, an insect pest of citrus fruits, and the insect parasitoid (*Aphytis*) that keeps it under biological control. A major feature of the models is their explicit recognition of differences among individuals of different age and developmental stage. This feature makes the models highly testable against experimental data, and a complementary program is under way to provide these data. The objective of this research is not only to develop and test models of these particular systems but, by exploring this range of systems, to develop general theory for population dynamics.

Relevance of Research Mathematical models to explain observed patterns in the dynamics of natural populations of organisms, such as plankton in lakes, insects in agricultural systems, and marine kelp beds, are being developed and tested. The research is indirectly related to other environmental problems. For example, models are needed to predict the effects of toxic substances on populations and communities in nature on the basis of the effects observed on individual organisms in the laboratory. The plankton models are designed precisely to translate changes in individual physiology into effects on populations. Furthermore, the test organism, *Daphnia*, is one of the standard organisms used as a toxicological bioassay. The models are also designed to predict changes in the dynamic behavior of populations responding to changes in the environment, for example, whether populations in midlatitude lakes will become less stable due to higher water temperature resulting from global warming. Because the research is, in part, an attempt to understand the features that distinguish successful biological control, which can replace insecticides, it may also help to reduce pollution by pesticides.

Project Title | Theoretical Ecology of Marine Populations

Principal Investigator | Jonathan Roughgarden

Research Institution | Hopkins Marine Station
Stanford University
Stanford, California 94305-6060
(415) 723-3648

Research Description

This project developed and is testing mathematical models that predict demographic change in an open population with space-limited recruitment, such as change of marine organisms with a sessile adult phase and a pelagic larval phase. Composition of barnacle-dominated communities in the intertidal zone of central California in the vicinity of Hopkins Marine Station is controlled by the arrival rate of larvae to potential sites. Processes that act after larvae arrive, such as predation and crowding, are of secondary importance. Focus is on developing mathematical models for a species population consisting of (1) sessile adults distributed among heterogeneous space-limited benthic habitats and (2) larvae in the surrounding water mass. These modeis treat the evolution of marine life histories and the conditions for regional coexistence of marine species. The research will also study the influence of predation on barnacle larvae by juvenile fish that live in offshore kelp forests. The kelp forest community is coupled to the intertidal community because of its effect on the rates of arrival of the larvae from intertidal organisms.

Relevance of Research

Dramatic fluctuations in the stocks of marine populations such as sardines, anchovies, shellfish, and squid have long been a source of economic loss, hardship to the general public, and confusion to scientists. The barnacle populations studied in this laboratory also show these fluctuations, and have proved to be a more tractable system to investigate than commercially exploited marine stocks. In the last 2 years, the key mechanism that causes dramatic fluctuations in barnacle populations has been identified. The mathematical population theory to predict when these fluctuations will occur has been refined. In a few years, it is projected that the age-old problem of understanding and predicting marine population fluctuations will be close to a resolution. Also, the ecological implications of pollution associated with offshore oil activities in central California will probably be predictable.

Project Title | Chaos and Microbial Systems

Principal Investigator | Mark Kot

Research Institution | Applied Mathematics
University of Washington
Seattle, Washington 98195
(206) 543-2584

Research Description

The last 10 years have seen a host of new discoveries in the field of nonlinear dynamics, especially regarding the phenomenon called chaos. A recurrent theme of this recent research is that seemingly random fluctuations often occur as the result of simple deterministic mechanisms. Hence, much of the recent work in nonlinear dynamics has centered on new techniques for identifying order in seemingly chaotic systems. When applied in ecology, these techniques have led to new insights for several systems, most notably various childhood epidemics. To determine the robustness of these techniques, chaos must, to some extent, be brought into the laboratory. Preliminary investigations of the forced double-Monod equations, a model for a predator and a prey in a chemostat with periodic variation in inflowing substrate concentration, suggest that simple microbial systems may provide the perfect framework for determining efficacy and relevance of the new nonlinear dynamics in dealing with complex population dynamics. This research examines the mathematical properties of the forced double-Monod model and provides an experimental investigation of the system.

Relevance of Research

This research promises new techniques for the analysis of populations with complex dynamics. In particular, by testing the biological efficacy of a series of new techniques from the field on nonlinear dynamics, this research offers hope for better understanding and prediction of the behavior of various notoriously erratic populations (e.g., insect pests and disease epidemics). In addition, this research m .y provide new insights into the effects of temporal heterogeneity and changing ambient conditions on the dynamics and evolution of simple biological communities. It will also provide a set of useful baseline data for toxicologists interested in community effects. Indeed, the work is being done in collaboration with a microbial ecologist and a protozoologist whose principal interests are biodegradation and the use of ciliates as indicator species for toxicants.

Project Title Dynamics of Recruitment-Subsidized Populations

Principal Investigator Hal Caswell

Research Institution Woods Hole Oceanographic Institution
Woods Hole, Massachusetts 02453
(508) 548-2751

Research Description Three models of subsidized populations are being developed and analyzed: density-independent demographic models, density-dependent demographic models, and metapopulation demographic models. Each model addresses a different aspect of the problem of recruitment subsidy, but they are tied together by subsidy. An analysis can be approached by determining the ways in which external subsidy and local population dynamics interact.

Density-independent demographic models: The immediate benefit of this research is a set of demographic methods that are applicable to relatively easily obtained real data and that extend classical life table methods to recruitment-subsidized populations. Like classical methods, these demographic analyses are valuable for the projection of current conditions, not prediction of future dynamics. However, such projections, properly interpreted, have proven a powerful tool in population biology; their extension to subsidized populations will be equally useful.

Density-dependent demographic models: The incorporation of density dependence makes a model simultaneously more realistic and more difficult to connect to real data. This research provides theoretically important results about the dynamic consequences of subsidy and density dependence by adding recruitment variability to Roughgarden's model and by incorporating other forms of density dependence.

Metapopulation demographic models: These models are presently limited to theoretical use. Empirical developments in this area will probably await the development of models linking subpopulations with actual physical oceanographic models. As theoretical tools, however, the proposed models permit questions about the interactions of life histories, spatial heterogeneity, and subsidy when all populations are viewed as contributors to a larval pool.

Relevance of Research Classical population dynamic theory presumes that recruitment of new individuals to the local population is due to reproduction of individuals in that population. This assumption fails for many marine organisms in which larvae may be dispersed for long distances relative to the scale on which populations are examined. These organisms include many of the most ecologically (and economically) important species in the marine environment. This research will provide a new theoretical framework for understanding these populations.

Project Title

Physiological and Ecological Implications of Coupled Heat-and-Water-Transport Mechanisms of Endotherms and Vegetation

Principal Investigator

Warren P. Porter

Research Institution

Department of Zoology
University of Wisconsin
Madison, Wisconsin 53706
(608) 262-1719

Research Description

Models can quantitatively predict effects of environmental change on animal growth and reproduction. This research develops general models of food, water, and heat balances for ectotherms and endotherms and tests predictions over a wide range of species in various environments. Thus, it identifies and quantifies important interactions between climate, physiology, and behavior in animal growth and reproduction. The research focuses on three activities: (1) it extends a current quantitative, general heat-and-water-transfer model, developed this past year and intended for the porous insulation of endotherms, to include the porous media of vegetation; (2) it tests the model's predictions for endotherm heat-generation requirements and water-loss rates for different insulations under conditions measured in the laboratory and in the field on various inanimate objects and live endotherms; and (3) it integrates the porous-media model with microclimate models already field tested in many environments to calculate heat and mass fluxes through low canopies of vegetation and the soil. The mechanistic model for endotherms will ultimately provide an enhanced means for generating and testing ecological hypotheses, such as environmental effects on herbivory rates, growth and reproduction rates, survival probabilities, and population dynamics.

Relevance of Research

This research has both theoretical and applied relevance. Theoretical aspects include—

- Ability to compute, while using first principles, how climate change affects growth and reproduction potential of wild animals.
- Prediction of the effects on growth and reproduction of the added stresses of diseases and toxicants as they interact with climates that also affect growth and reproduction.
- Prediction of changes in distribution limits of animals for any climate scenario.
- Determination of optimal behaviors to assess the feasible set of such behaviors for optimal growth and reproduction under the effects of climate variation.
- Capability to calculate altered food requirements that result from climate change.

Applied aspects of this project include—

- Computation of the effects of climate change on domestic animal production. These models have been tested successfully on both cattle and pigs. Heat stress or cold stress effects can substantially modify their growth potential or milk production.
- Assessment and consequences of management decisions on energy development that alters habitat and microclimates needed by animals for survival, growth, and reproduction. Because the models are mechanistic, landscape modifications that alter solar, wind, or other environmental variables can be used to compute new microclimate conditions and how the animals will respond in terms of food and water requirements and growth and reproduction potential.
- Amelioration simulations can be done to determine the most effective restoration tactics while creating microhabitats suitable for promoting the return or introduction of desired species in areas that may have been altered during energy development.

EXPERIMENT/SAMPLE DESIGN

Project Title Designs for Environmental Field Studies

Principal Investigators J.M. Thomas[1] and L.L. Eberhardt[2]

Research Institution Environmental Sciences Laboratory
Battelle Pacific Northwest Laboratory
Richland, Washington 99352
[1](509) 376-7982
[2](509) 376-8265

Research Description This project concerns ways to correct shortcomings of current field studies in ecology and environmental science. The research is developing suitable sampling designs based on the appropriate objectives for field work. Suitable designs for several classes of sampling have been developed in very different fields and are, thus, largely unknown to ecologists and environmental scientists. Hence, an important part of the research is devoted to adapting results from these other fields (e.g., geostatistics and industrial research) for use in ecological studies. The research investigates (1) replicated experiments, (2) unreplicated experiments, (3) intervention analysis, (4) survey sampling, (5) analytical sampling, (6) observational studies, (7) sampling for pattern, and (8) sampling for modeling. The project combines elements of experimental design, survey and analytic sampling, and modeling with geostatistical and biometrical methods to develop or adapt cost-effective innovative field statistical methods for the study of environmental phenomena. The technology is being developed to provide a firm scientific basis for field studies required to understand the environmental behavior of energy-derived chemicals. The project emphasizes developing field designs based on clear objectives and approaches that incorporate sampling theory rather than classical experimental designs. A portion of the research is devoted to expanding and adapting methods from geostatistics and industrial research as examples.

Relevance of Research Recent national concerns include hazards from chemical waste sites, subsurface transport of pollutants, and possible landscape-level effects due to global changes. Approaches to study these issues and other field problems in ecology are limited by the lack of theory and suitable designs for sampling contaminants and populations in time and space. This program provides a firm scientific basis for the myriad of field studies required to understand large-scale events, the environmental behavior of energy-induced chemicals, effects on populations, and landscape-level sampling. The research places strong emphasis on developing field designs based on clear objectives, approaches that incorporate sampling theory rather than classical experimental designs, and quantitative issues in the use of modern technology (e.g., satellite imagery) to aid in solving global problems.

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