

Frontiers of Ecology

JOHN N. THOMPSON, O. J. REICHMAN, PETER J. MORIN, GARY A. POLIS, MARY E. POWER, ROBERT W. STERNER, CAROL A. COUCH, LAURA GOUGH, ROBERT HOLT, DAVID U. HOOPER, FELICIA KEESING, CHARLES R. LOVELL, BRUCE T. MILNE, MANUEL C. MOLLES, DAVID W. ROBERTS, AND SHARON Y. STRAUSS

Ecological research is entering a new era of integration and collaboration as we meet the challenge of understanding the great complexity of biological systems. Ecological subdisciplines are rapidly combining and incorporating other biological, physical, mathematical, and sociological disciplines. The burgeoning base of theoretical and empirical work, made possible by new methods, technologies, and funding opportunities, is providing the opportunity to reach robust answers to major ecological questions.

In December 1999 the National Science Foundation convened a white paper committee to evaluate what we know and do not know about important ecological processes, what hurdles currently hamper our progress, and what intellectual and conceptual interfaces need to be encouraged. The committee distilled the discussion into four frontiers in research on the ecological structure of the earth's biological diversity and the ways in which ecological processes continuously shape that structure (i.e., ecological dynamics). This article summarizes the discussions of those frontiers and explains why they are crucial to our understanding of how ecological processes shape patterns and dynamics of global biocomplexity. The frontiers are

1. Dynamics of coalescence in complex communities
2. Evolutionary and historical determinants of ecological processes: The role of ecological memory
3. Emergent properties of complex systems: Biophysical constraints and evolutionary attractors
4. Ecological topology: Defining the spatiotemporal domains of causality for ecological structure and processes

AS ECOLOGICAL RESEARCH ENTERS A NEW ERA OF COLLABORATION, INTEGRATION, AND TECHNOLOGICAL SOPHISTICATION, FOUR FRONTIERS SEEM PARAMOUNT FOR UNDERSTANDING HOW BIOLOGICAL AND PHYSICAL PROCESSES INTERACT OVER MULTIPLE SPATIAL AND TEMPORAL SCALES TO SHAPE THE EARTH'S BIODIVERSITY

Each of the four research frontiers takes a different approach to the overall ecological dynamics of biocomplexity, and all require integration and collaboration among those approaches. These overlapping frontiers themselves are not necessarily new. Within each frontier, however, are emerging questions and approaches that will help us understand how ecological processes are interconnected over multiple spatial and temporal scales, from local community structure to global patterns.

Research frontier 1: Dynamics of coalescence in complex communities

We use the term *community coalescence* to refer to the development of complex ecological communities from a

John N. Thompson (e-mail: thompson@biology.ucsc.edu) is a professor in the Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064. O. J. Reichman is director of the National Center for Ecological Analysis Synthesis, 735 State Street, Santa Barbara, CA 93101. Peter J. Morin is a professor in the Department of Ecology, Evolution, and Natural Resources, Cook College, Rutgers University, New Brunswick, NJ 08901-8551. Gary A. Polis (deceased) was professor and chair of the Department of Environmental Sciences and Policy, University of California, Davis, CA 95616. Mary E. Power is a professor in the Department of Integrative Biology, University of California, Berkeley, CA 94720. Robert W. Sterner is professor and head of the Department of Ecology Evolution and Behavior, University of Minnesota, St. Paul, MN 55108. Carol A. Couch is a senior research scientist in the Water Resources Division of the US Geological Survey, Norcross, GA 30360-2824. Laura Gough is an assistant professor in the Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487-0206. Robert Holt is a professor in the Department of Ecology and Evolutionary Biology, Natural History Museum, University of Kansas, Lawrence, KS 66045. David U. Hooper is an assistant professor in the Department of Biology, Western Washington University, Bellingham, WA 98225-9160. Felicia Keesing is an assistant professor in the Department of Biology, Bard College, Annandale, NY 12504. Charles R. Lovell is a professor in the Department of Biological Sciences, University of South Carolina, Columbia, SC 29208. Bruce T. Milne and Manuel C. Molles are professors in the Department of Biology, University of New Mexico, Albuquerque, NM 87131. David W. Roberts is an associate professor in the Forest Resources Department, Utah State University, Logan, UT 84322. Sharon Y. Strauss is an associate professor in the section of Evolution and Ecology, University of California, Davis, CA 95616.

regional species pool. This coalescence depends on interactions among species availability, physical environment, evolutionary history, and temporal sequence of assembly. Ecologists have made important strides in understanding the process of community coalescence, but it will take even greater integration of approaches for us to be able to confidently predict the pathways or endpoints of community assembly (Belyea and Lancaster 1999, Gotelli 1999, Weiher and Keddy 1999). So far, we cannot predict which species are likely to invade or to be lost from particular natural communities, although some patterns are beginning to emerge (Petchev et al. 1999). We also have much to learn about community responses to perturbations at different stages in development.

Much of what we do know comes from a handful of easily studied systems, whereas the functioning of communities undoubtedly also depends heavily on little-studied hidden players, such as microbes, fungi, and soil invertebrates (de Ruiter et al. 1995). Indeed, many attempts to create or restore communities (e.g., freshwater wetlands or salt marshes) fail for reasons that remain poorly understood. Until we can fill these fundamental gaps in our knowledge, human impacts on community patterns will remain hard to predict.

Research conducted over the last decade suggests what kinds of studies are needed to fill the gaps. Progress will almost certainly depend on developing new ways to simplify the study of complex communities. Focusing on functional groups or other as yet undeveloped constructs may help. We are also aware that we need to learn far more about the systematics of many smaller or cryptic organisms, which may form links that are crucial to our understanding of community coalescence. The difficulty of linking important ecosystem functions to key taxa and interspecific interactions is a particular challenge.

Research in five key areas, described below, could provide important insights into the community assembly process.

Functional traits and community composition. As we study communities that are increasingly a mix of native and introduced taxa, we need to find out whether coevolved species or local populations differ from coevolutionarily naive populations in the strength or nature of their interactions during or after community assembly. We need to improve our ability to pinpoint the traits of species that affect the probability of invasion or extinction within developing communities (Pimm 1989, Rejmánek and Richardson 1996, Belyea and Lancaster 1999). Moreover, we need to further our understanding of how the importance of those traits depends on existing species composition, critical thresholds (e.g., species richness, functional group composition), and history of a community (Rejmánek 1989, Burke and Grime 1996, Levine and D'Antonio 1999).

Pathways toward community coalescence. For any pool of potential community members there are many

possible assembly sequences and endpoints. The diversity of initial sequences is less problematic if many of the alternative pathways tend to converge on a limited subset of endpoints. To that end, we need to find out whether developing communities move toward single or multiple points or states (attractors). Past some stage of assembly, community composition may become canalized, but it may be highly susceptible to perturbations in the early stages of coalescence. Anthropogenic change may limit pathways of community development by changing the physicochemical environment, altering biogeochemical cycles, or changing the genetic structure of populations. Global homogenization of the species pool may itself alter the pathways or endpoints of community assembly, reshaping both short-term and long-term successional patterns across landscapes.

Functional groups. Ecologists recognize that the concept of functional groups is a valuable tool for simplifying community complexity to manageable levels. Currently, most groups are defined in a system-specific way (Wilson 1999) based on biochemical, morphological, or trophic criteria (Vitousek and Hooper 1993, Hooper and Vitousek 1997, Naeem and Li 1997, Tilman et al. 1997), although some attempts have been made to develop general classifications (Grime et al. 1997). Each of these attempts has helped us identify the advantages and disadvantages of different approaches. Together, they are moving us toward the development of robust frameworks that work across multiple taxa and ecological communities. Those advances should ultimately help us to understand how functional group structure shapes assembly dynamics, as well as to evaluate how different configurations of functional groups affect the development of communities or the dynamics of ecosystems (e.g., rates and trajectories of community development with and without nitrogen-fixing species).

Hidden players. Community assembly almost certainly depends upon cryptic invertebrate, microbiological, and mycological groups, which include a vast array of free-living species, parasites, and mutualistic symbionts. These groups and interactions have historically been ignored or unrecognized because of technological limitations and biases in the training of ecologists. Many microbial species cannot yet even be cultured. Nevertheless, they may play a keystone role in community development and function, and their absence may be responsible for some failed attempts at community restoration (Wall Freckman et al. 1997, Brussaard 1998). The importance of these hidden players may become apparent only when they become problems, as sometimes happens when we alter community structure. Lyme disease, for example, may be the result of the emergence of a hidden player in response to changes in community composition and landscape patterns (Jones et al. 1998).

Part of our challenge will be to determine how the structure of microbial diversity should be incorporated into different kinds of analyses of the local, regional, and global



Figure 1. *The Salmon River within the large wilderness core of Idaho. The few remaining relatively pristine landscapes worldwide will become increasingly important for testing hypotheses at the frontiers of ecology. These unfragmented landscapes are our only way of testing hypotheses on the dynamics and trajectories of ecosystem and evolutionary processes acting on extant species over long time scales and across broad geographic areas.*
Photo: John Thompson.

dynamics of ecological processes. Traditional definitions of species and traditional metrics of distribution and abundance often make a poor fit with the structure of microbial populations and communities.

Our research choices have been biased not only toward particular taxa but also toward particular communities. We have detailed community assembly information on only a small number of well-studied kinds of communities (e.g., successional fields, temperate lakes, rocky intertidal shores). Studies of underrepresented communities, taxa, and interactions will together provide important insights into general patterns in the assembly process (e.g., roles of particular kinds of microbial interaction or mutualistic interaction).

Restoration. The best measure of our understanding of any complex system is whether we can reconstruct it from its parts (Jordan et al. 1987). Successful restoration of sustainable communities, and de novo creation of persistent complex systems that provide essential ecosystem services in novel environments, are therefore the true tests of our understanding of community dynamics. Those tasks, in short, constitute the shared frontier of community ecology and ecological restoration. We need to know which aspects of community structure are restorable once disassembled and which are not. Although our understanding of what is restorable is limited, our societies are nonetheless moving apace to manipulate community assemblages worldwide (Simberloff et al. 1997). We must therefore continue to work toward a more

comprehensive theory of community coalescence if we are to succeed in efforts to mitigate the effects of invasive species on local communities and to make those communities less prone to disruption. The deliberate introduction of species, which takes place now in biological control efforts, will surely be less risky once we understand how to enhance the control of species through the assembly of persistent but self-limiting subwebs. Similarly, bioremediation efforts will benefit from understanding how to develop persistent, self-limiting assemblages of species that accumulate or degrade toxic wastes.

Research frontier 2: Evolutionary and historical determinants of ecological processes

The genetic and evolutionary structure of organisms, in combination with the recent history of environmental events, continually shape the dynamic patterns of community coalescence outlined in frontier 1. Biology is a science strongly influenced by historical events. Evolution and environmental history impose “ecological memory” on communities, introduce time lags in ecological processes, and constrain the trajectories of community coalescence in ways that are poorly understood. Ecological memory—the result of past environmental conditions and subsequent selection on populations—is encoded in the current structure of biological communities and reflected in the genetic structure of species. It affects how communities assemble, and it may also affect the likelihood that they can be restored once

disassembled. We therefore need a much better understanding of which aspects of phylogeny, ongoing evolution, and recent history are most important in shaping current ecological processes and patterns across landscapes.

The combined roles of phylogeny and ongoing evolution. Although biologists commonly divide the temporal continuum into ecological time and evolutionary time, evolution shapes ecological processes across all time intervals. The phylogenetic history of species creates large-scale patterns in the ecological relationships of taxa and combines with rapid evolution over the scale of decades to generate ongoing ecological dynamics. We need to answer six crucial questions if we are to develop a theory of ecology that takes into account the genetics and evolution of organisms.

Phylogenetic structure of ecological processes. How does the shared phylogenetic history of species shape ecological processes? Because of shared phylogenetic history, species cannot be treated as independent units in their ecological roles. We know, for example, that ecological specialization is phylogenetically constrained (Futuyma and Mitter 1996, Webb 2000). A few studies have analyzed how shared species' traits and historical biogeography combine to constrain and shape community and ecosystem structures. For example, analysis of the phylogeny of Caribbean anole lizards casts doubt on the overall applicability of a widely cited ecological theory, the taxon cycle (Butler and Losos 1997). Recent analyses of rain forest in Borneo indicate that more closely related species were found in the same microhabitats more often than could be explained by chance alone (Webb 2000). We need similar analyses across taxa and ecosystems to further integrate phylogenetic nonindependence into community and ecosystem ecology.

Rapid evolution and ecological dynamics. To what extent are succession, population dynamics, and ecosystem dynamics—historically considered to be solely ecological processes—governed by rapid evolutionary change in species and their interactions? There are dozens of examples in which ecologically important traits of species are known to have evolved during the past century (Thompson 1998, 1999). Rapid evolution of bill morphology in Galapagos finches, wing color in peppered moths, and pesticide resistance in many taxa are well-known examples that highlight the speed with which natural populations can evolve when subjected to environmental change. These evolutionary changes have the potential to ripple throughout communities. For example, the recently discovered rapid evolution of *Daphnia* in response to pollution in Lake Constance may change phytoplankton dynamics in ways that are important to community function (Hairston et al. 1999).

Coevolution and ecological dynamics. How does the history of species cooccurrence shape ecological processes, community function, and community stability and invasibility? Use of molecular markers coupled with new analytical techniques

such as coalescence theory may allow us to estimate the length of time that locally and regionally interacting species have cooccurred (Pellmyr et al. 1998). These techniques could enable us to determine whether populations, species, and communities that share a history of cooccurrence exhibit properties different from those created largely from recent invasions or restoration efforts. They will help us determine whether long-term coevolution of taxa affects community properties such as invasibility, nutrient cycling, and productivity.

Scale of evolutionary dynamics. How do landscape structure and genetic structure act together in shaping ecological processes? Ecologists are beginning to look hard at how the spatial scale of ongoing evolution and coevolution shapes ecological dynamics. Species are groups of genetically differentiated populations connected by various levels of gene flow. Adaptations developed within local communities can spread to populations in other communities, thereby altering local ecological dynamics. Natural and anthropogenic fragmentation of populations restricts the exchange of individuals among communities both historically and currently. We are just beginning to understand how the landscape structure of fragmentation interacts with the genetic configuration of species and ongoing evolution to shape ecological processes at local, regional, and continental scales. We need a refined theory of spatially structured evolutionary dynamics to assess the overall effects of increased anthropogenic fragmentation on communities.

Genetic diversity and ecological dynamics. How does genetic diversity within species shape the temporal dynamics of populations, trophic interactions, and energy flow in ecosystems? By incorporating the effects of genetic diversity per se into our models of the temporal dynamics of ecosystem structure and function, we may better understand and predict ecological systems. The study of plant hybrid zones has given us a glimpse of the potentially far-reaching effects of the structure of genetic diversity on community dynamics (Whitham et al. 1999). Particular genotypes or hybrids of some species are much more vulnerable to herbivores or are more productive than other genotypes or either of the parental species. Moreover, some hybrids and genotypes support greater diversity and biomass of insect herbivores, birds, and other species, thereby becoming local foci of diversity and supporting distinct food web interactions.

Genomics of ecological dynamics. How do genomic content and patterns of gene expression shape species distributions, species interactions, and responses to changing environments? We are just starting to evaluate the ways in which chromosome number shapes large-scale patterns in community structure and dynamics. From a small number of studies we know that chromosome number is tied to ecologically important attributes of taxa, such as species distributions (e.g., the proportion of polyploid plant species increases with latitude), invasiveness, and susceptibility of



Figure 2. *The fragmented wet tropics of northern Queensland, Australia, north of Cairns. Similar landscapes now characterize most terrestrial environments worldwide, illustrating the need for understanding the dynamics of population, community, ecosystem, and evolutionary processes in environments whose boundaries are sharp and constantly changing across large spatial and temporal scales. Photo: John Thompson.*

plants to herbivores (e.g., moths on saxifrages) (Rosenzweig 1995, Thompson et al. 1997). Thus, the evolutionary genomics of component species may have strong impacts on the ecological functioning of communities.

The role of environmental history and temporal variability. Ecological research needs to build on past efforts to integrate processes acting across different time scales. All environments vary through time at scales from very short (hours, days) to long (decades, centuries, millennia). Because of this temporal variability, we often cannot understand communities without understanding past events or processes. We know that three components of environmental history and temporal variability appear to be particularly important in shaping community dynamics: variability in productivity and the input of resources; variability in species composition, abundance, and interaction strength; and variability in key abiotic events. The impact of these factors can change over different time scales, shaping species composition, abundance, and food web interactions in the short term (e.g., via recent invasion), medium term (range expansion and contraction), and long term (historical biogeography).

Historical variability in productivity or resource input. Resources vary in availability over time in all communities through abiotic (e.g., wet versus dry seasons; El Niño versus La Niña years) and biotic influences (mast years in long-lived plants, pig wastes flowing into watersheds) (Polis et al. 1996). Such variation has been characterized by ecologists

working on particular taxa or communities. Nevertheless, we are only in the early stages of developing a general body of theory on how past periodic or pulsed productivity affects the dynamics of populations, interactions between resources and consumers, food webs, communities, and ecosystems.

We need to continue to work toward a synthetic framework for explaining how temporally variable productivity influences food web processes, community dynamics, and ecosystem function. For example, masting events and periodic emergence of insects (e.g., cicadas) can greatly alter species interactions and community dynamics for years (Jones et al. 1998). Long periods between pulses of high productivity reduce consumer abundance, consequently impeding resource suppression at the next productive period. This process appears to underlie the evolution of masting in bamboos and trees and synchronous reproduction in insects and ungulates (Janzen 1976).

In general, periodic pulses of productivity (e.g., good versus bad years or seasons) may produce resource reserves that last for varying periods before they are depleted, altering food web dynamics long after the productivity pulse (Noy-Meir 1974, Sears et al. in press). For example, El Niño rains (or La Niña drought) may stimulate or depress terrestrial productivity, thereby allowing subsequently high or low abundances of consumers and altering interactions between resources and consumers (Polis et al. 1997). On smaller spatial scales, the pattern of local competitive outcomes in forests may depend on the pattern of tree falls, old allelopathic footprints, and past local patterns of

nutrient depletion or regeneration, each of which may produce long-lasting changes in local soil chemistry.

Historical variability in species composition, abundance, and interaction strength. We are beginning to disentangle the ways in which past community configurations shape current processes. We know, for example, that the effects of introductions of new species into communities can depend on past presence of particular taxa. Introduction of cows into intermountain western North America led to effects on grassland and steppe communities that were far different from those resulting from similar introductions east of the Rockies. These differing impacts came about in part from differences in the history of association of these grasslands with bison and the selection these large mammals imposed on plant taxa. In addition, short-term irruptions of species can produce long-lasting effects. The irruption of rinderpest in some African grasslands resulted in a single flush of recruitment of acacias during this century. The acacias are still extant, yet current ecological conditions or their recent life history statistics (e.g., measurement of intrinsic rate of natural increase) do not account for their presence.

Historical variability in key abiotic events. Erratic large-scale disturbance regimes can leave profound ecological legacies that may propagate historical echoes. Volcanoes, hurricanes, El Niño–southern oscillation events, or interdecadal oscillations all reshape biological communities in ways that have long-lasting effects. For example, interdecadal changes in anchor ice play a major role in altering the abundance, composition, and interaction dynamics of the entire bottom community in the Antarctic (Dayton 1989). We must strive to develop a fuller appreciation of when and how these major periodic environmental events are important in shaping global and regional patterns in ecological processes.

Research frontier 3: Emergent properties of complex systems

The evolutionary and historical determinants of ecological processes outlined in research frontier 2 are in turn shaped in large part by the laws of physical science. Hence, the third frontier is to understand how the joint evolutionary forces acting on an entire species assemblage result from constraints imposed by biophysical processes.

Phenotypic traits are products of adaptive evolution operating within bounds set by physical and chemical constraints. Important progress in determining how these constraints affect the morphology and behavior of individual species has been registered in the subdisciplines of physiological and functional ecology. Today's research frontier is the expansion of this viewpoint to collections of species and communities and ecosystems. We need to know how specific evolutionary responses at the species level produce the collective morphology (physiognomy) and behavior (ecosystem function) of ecosystems. One central question is whether first principles of physics, chemistry, and

evolution by natural selection can successfully predict the composition, structure, and functioning of ecosystems. If so, evolutionary first principles could enhance ecosystem study. Reciprocally, advances in studies of matter and energy flow can provide the information necessary to realistically assess biophysical constraints on evolutionary change.

If we imagine a community as a set of species plotted in multidimensional phenotypic space, then enclosing this space is a set of boundaries and constraints imposed by the principles of energy and thermodynamics. Matter devoted to one use is unavailable for other uses, and these constraints generate evolutionary tradeoffs. Selection maximizes fitness within those constraints. In the terminology of dynamic systems theory, the result is an attractor, a condition (such as a set of phenotypes) toward which a system (such as a community) is drawn over (evolutionary) time.

As each organism responds to its environment in a manner prescribed by its genome and the specifics of its biophysical and biotic environment, it simultaneously modifies that environment. The result is a coupled, complex, dynamic system of organism and environment, wherein natural selection optimizes the fitness of populations amid a continually changing, biotically driven environment. If a single species of plant evolves to have larger leaf area, a host of allometric tradeoffs within that species come into play, such as corresponding increases in sapwood conducting volume. The cumulative effect of these changes may be an alteration in how resources are used within a community. Material and energy fluxes for competing species and consumers of that plant may in turn also be affected.

An example of an attractor resulting from biophysical properties is the 0.75 power law for metabolism in endothermic animals, which states that whole-body metabolic rate scales with body mass to the 0.75 power. Although there has been turnover of species along this curve over time, the physical basis of this power law ensures that the curve itself has remained fixed. Such an evolutionary attractor works through a combination of physical principles and evolutionary optimization. Phenotypes that deviate from this attractor are at a significant disadvantage compared with those near the attractor.

The frequency distributions of body mass in mammals, which demonstrate a unimodal relationship, may be another example. Brown (1995) suggested that modal mass corresponds to an evolutionary optimum (attractor) for a given body plan. Body mass may be governed by a tradeoff between resource harvest ability and bioenergetic patterns determining the rate at which resources can be turned into reproduction. Deviations from the optimum may be driven by niche partitioning. Ritchie and Olff (1999) used spatial scaling laws to describe how species of different sizes find food in patches of varying size and resource concentration. They derived a mathematical rule for the species that share resources and used the rule to develop a predictive theory of the relationship between productivity and diversity. Spatial scaling laws, they argued, provide potentially

unifying first principles that may explain many important patterns in species diversity.

Biochemical constraints may also result in an evolutionary attractor on life history evolution. Evidence for such constraints is accumulating through studies of ecological stoichiometry, which considers patterns in element concentration among different species (Sternner 1995). Recent studies have indicated that rapid growth in biomass requires an element composition high in phosphorus (P), a result of the element composition of anabolic biochemical machinery—in particular, ribosomes (Elser et al. 1996). Thus, life history evolution is constrained in a phenotypic space that includes phosphorus as one of its axes: High growth rate depends upon high P content. Another stoichiometric example is the evolution of structural material, such as wood or bones, in which different biochemical solutions to the same or similar structural problems have been achieved. Hence, we see alternative chemical signatures in living organisms. The larger the organism, the greater the reliance on carbon (C) (for wood) or calcium (Ca) and phosphorus (for bone), generating an attractor in a phenotypic space that includes elements such as C, Ca, or P as well as organism body size.

Specific research questions. We need to answer several questions about the physical basis of evolutionary attractors. Among them are these:

- How are species arranged as collections in phenotypic space bounded by biophysical constraints?
- How do adaptive solutions vary as species diversity varies within those constraints?
- Can different, coherent sets of community members become established as multiple stable states, or does each situation engender a specific ecological and evolutionary solution (based on ecological stoichiometry or similar constraints)?
- What effect does fitness maximization of individuals have on the collective behavior of all species and on the fluxes of matter and energy within these collections?
- Can first principles be used to predict the statistical distribution of species traits, not just a single optimum? Can that distribution be extrapolated to predictions or estimates of diversity?

We cannot begin to cross this frontier successfully unless we find the means to perform rigorous experimental tests or find other ways to test hypotheses. Multispecies correlations of phenotypic traits will be relatively easy to find, but testing among competing hypotheses for these broad-scale patterns will require considerable ingenuity. Experimental tests of some evolutionary hypotheses are impossible for all but the smallest (and most quickly reproducing) organisms, but microbial taxa make excellent experimental tools for answering some of these questions. For most other taxa,

less direct means of testing mechanistic hypotheses will be necessary.

New techniques. New approaches in the study of structural and functional genomics can further this highly integrated view of evolution and ecosystems. A community is composed of suites of genes that are collected into epistatic groups, these into genomes, and finally genomes into communities. Breakthroughs in gene sequencing and in measuring patterns of gene expression should make it increasingly practicable for ecologists to study the relationships between biophysical constraints and evolutionary attractors. For example, studies have described the patterns of expression of 6347 genes in mice raised under caloric restriction (Lee et al. 1999). Caloric restriction retarded aging by causing a metabolic shift toward increased protein turnover and decreased macromolecular damage. These experiments provide a glimpse of a single genome's response to the changed availability of energy. They suggest intriguing links between genomics and energy and nitrogen fluxes. We need to explore how species' genomes respond to each other as material and energy availability change. Such studies can be viewed as ecological, community, or even ecosystem genomics.

Research frontier 4: Ecological topology

Frontiers 1, 2, and 3 require that we reevaluate the scale of ecological processes and the analytical methods by which we study them. We need to develop a way of evaluating how our scales of information (scope and resolution in space and time) affect our understanding of ecological processes—that is, an ecological topology. We can think of this ecological topology as a study of the domains of causality. For instance, what are the factors that control rates of primary production by native plants on ancient lava surfaces in Hawaii? The most important controls may be local (e.g., competition among neighboring plants), regional (e.g., grazing by wandering goats introduced by Europeans centuries earlier and sustained by productivity of the larger surrounding landscape), or even global (set by the levels of phosphorus in eolian dust from Central Asia, mobilized during the last glacial period) (Jackson et al. 1971, Chadwick et al. 1999). The appropriate domains of causality in many ecological studies could extend far beyond previously assumed spatial and temporal bounds.

We therefore need a unified understanding of the spatial and temporal context of ecological interactions, such as the magnitude and importance of cross-habitat fluxes of matter, energy, and information, sometimes acting over very large scales. Even our understanding of fundamental matters such as the structure of food webs generally lacks a spatiotemporal context, strongly limiting our ability to explain their origin, maintenance, or consequences. We suggest building an ecological topology that addresses these needs. Doing so requires characterizing patterns of movement of individuals (Holt and Gaines 1992, Holt 1993) and flow of materials



Figure 3. Coalescence of a new, complex plant community of native and introduced species at Tejon Pass, California. The community includes a mix of annual Mediterranean grass species and a diverse array of native annual wildflowers. Before invasion by the introduced grasses, the community was probably dominated by perennial, tussock-forming grasses, along with annual grasses and forbs. Photo: Courtesy of Frank Davis, University of California, Santa Barbara.

(Power and Rainey in press) across space and through time (Polis et al. 1997). This frontier is consistent with today's great need for scaling up from local processes to much larger ones, including the planetary scale. Global change is one of the most pressing issues in ecology today. Understanding the topology of causation of ecological patterns and processes could provide a formal structure for linking studies at the local scale to larger ones.

We already have some tools, and could soon develop others, to investigate and characterize the bounds of such spatiotemporal domains. Genetic and isotopic tracers for following the movement of matter and organisms within and across ecosystem boundaries are becoming more accessible. We have new satellite and ground-based technologies that expand our ability to capture and analyze spatial data. With these conceptual and technical tools, we can address a broad range of important ecological problems, such as those that follow.

Choosing the right spatial and temporal context.

How do different spatial and temporal domains of causality combine to produce local community patterns and processes? Moreover, how far back in time or out into the spatial landscape must we probe to understand local phenomena or interactions? We need to find out just how far we should expand the domains of our search if we are to interpret ecological patterns and processes correctly.

Identifying the rules. What rules govern the origin and maintenance of ecological topologies? Clearly, some general rules govern the geometries of circulatory systems or the drainage networks of watersheds. This is an area of active

research in scientific fields outside ecology, and some of the methods of those fields could inform us about the bounds of ecological systems.

Changing the bounds. How will ecological communities change when their bounds change? If there are natural constraints on the bounds of domains of ecological processes, will truncating or stretching them change system behavior, stability, or sustainability? This is a crucial consideration, given human domination and rearrangement of ecosystems. For example, the California water system has been called the most massive rearrangement of nature ever attempted. Interbasin water transfers are now common throughout many arid regions of the world, depleting or artificially augmenting local ecosystems and groundwater systems. Release of carboniferous fossil fuels back into the active global carbon cycle is another example of human domain stretching along a deep temporal axis. Our global homogenization of species could also be considered in this light. Humans, however, do not always stretch causality domains. Sometimes we greatly contract them, as when we replace wild populations of salmonids, which harvest huge areas of ocean production, with caged fish that feed only in the mouths of estuaries. It is worth exploring whether causality domain theory can enhance our ability to predict the longer-term consequences of ecological distortions of various types and magnitudes.

Focus on these ecological topologies will require a change in how ecologists typically think of ecosystems. Conventionally, the term *ecosystem* refers to a particular contiguous unit of the landscape. The system has inputs and outputs and internal dynamics. Most management practices similarly focus on ecological processes and patterns defined by such habitat units.

Nevertheless, many, if not most, ecological processes can be envisaged as caused by a set of rules, each of which operates over different spatial and temporal scales. Understanding those rules is among our great current challenges.

Meeting the challenge

The challenges ahead will require new ways of working together, new tools, and greater access to an ever growing number of databases.

Collaboration and integration. No single scientist has depth enough across all the physical and biological sciences to address the questions at the frontiers. Therefore, we must foster research collaborations among scientists who are trained to understand the language of one another. Meeting that challenge will require renewed effort to make sure that ecologists are well-grounded in earth sciences and mathematics, and physical scientists solidly grounded in the theory of ecology.

In addition, stronger links between ecology and evolutionary biology must be forged across all the frontiers. Despite the formation of departments of ecology and evolutionary biology in many universities during the last 30 years, there remains a major gap between these disciplines. Relatively few ecologists have ever had a formal course in evolutionary processes, and very few have ever had advanced training in evolutionary theory and methods. Similarly, few evolutionary biologists have much advanced training in current ecological theory and methods. Incorporating an evolutionary framework into ecological research requires that we train scientists to be well versed in both ecological and evolutionary theory.

Analogously, there is a need to strengthen the links between ecosystem and community ecology. Understanding how biological communities shape, and are shaped by, physical environmental processes will transpire as the disciplinary barriers between ecosystem ecology and community ecology break down.

The need for stronger links between systematics and ecology is evident for all taxa, but it is especially critical for microbial groups. We need to turn out a generation of biologists who are well grounded both in microbial ecology and microbial systematics. These will be scientists capable of grappling with the complex structure of microbial taxa in an ecological context. We are only in the early stages of what will become a major field of study: how microbial diversity contributes to the dynamics of biocomplexity. The same needs hold for studies of the systematics and ecology of cryptic invertebrates and fungi.

Analytical tools. The mathematical and statistical constructs used in ecological research come mostly from linear theory. In contrast, many ecological processes are governed by nonlinear dynamics, threshold effects, and more complex relational structures. We must continue to work on

developing ecological theory that builds on the structure of empirical results in ecology.

Access to research and monitoring databases. We also need ecologists trained to manage large databases, who can organize the storehouse of past ecological data, mine it for new results, and make it accessible to others. Lack of ready access to the already available mass of ecological data is a major hurdle in ecological analysis. The experience of dozens of working groups at the National Center for Ecological Analysis and Synthesis in Santa Barbara, California, who are attempting to summarize and compare data collected over decades for a wide variety of purposes, confirms this need. Hence, the need for stronger links between empirical ecologists and database managers will continue to grow as new ecological data are gathered for ever-changing questions.

The existing storehouse of ecological data includes not only the results of individual studies but also the many databases that come from environmental monitoring efforts. Maintenance of these monitoring efforts is important if we are to understand how past environmental events shape current ecological processes. Monitoring efforts, however, are useful for ecological analyses only if their results are readily accessible to ecologists.

Moreover, to work with diverse data sets, collection methods and data entry methods must be standardized wherever possible. Techniques continue to change, and different methods are needed for different ecological situations. Nevertheless, we need to take a fresh look at some of the common methods used in studies within subdisciplines and attempt standardization.

Conclusion

Ecological research is undoubtedly entering a new era, building on a firm base of advancements in our ecological knowledge achieved in recent years. Each of the frontiers of ecology requires increased collaboration and technology if we are to understand how the complexity of ecological processes continues to reshape the earth. Most of the unresolved challenges in ecology arise from incomplete understanding of how biological and physical processes interact over multiple spatial and temporal scales. These challenges permeate the four interrelated research frontiers we have identified. Crossing the frontiers demands strong cross-disciplinary training and collaboration, coordination of observational and experimental approaches across large scales, incorporation of new technologies, and greater access to the growing database of ecological results. Developing the means to cross the frontiers is essential if the field of ecology is to move forward as a predictive science.

Acknowledgments

We are grateful to Scott Collins, William Michener, and Margaret Palmer, program officers for the National Science Foundation, for initiating this effort to assess the frontiers of ecology. We are also grateful to three anonymous

reviewers for very helpful and thoughtful reviews. This work was supported by NSF grant 97-07781 to J. N. T.

References cited

- Belyea LR, Lancaster J. 1999. Assembly rules within a contingent ecology. *Oikos* 86: 402–416.
- Brown JH. 1995. *Macroecology*. Chicago: University of Chicago Press.
- Brussaard L. 1998. Soil fauna, guilds, functional groups and ecosystem processes. *Applied Soil Ecology* 9: 123–135.
- Burke MJW, Grime JP. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776–790.
- Butler MA, Losos JB. 1997. Testing for unequal amounts of evolution in a continuous character on different branches of a phylogenetic tree using linear and squared-change parsimony. *Evolution* 51: 1623–1635.
- Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* 397: 491–497.
- Dayton P. 1989. Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. *Science* 245: 1484–1486.
- de Ruiter PC, Neutel A, Moore JC. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269: 1257–1260.
- Elser JJ, Dobberfuhl D, MacKay NA, Schampel JH. 1996. Organism size, life history, and N:P stoichiometry: Towards a unified view of cellular and ecosystem processes. *BioScience* 46: 674–684.
- Futuyma DJ, Mitter C. 1996. Insect–plant interactions: The evolution of component communities. *Philosophical Transactions of the Royal Society of London B* 351: 1361–1366.
- Gotelli NJ. 1999. How do communities come together? *Science* 286: 1684–1685.
- Grime JP, et al. 1997. Integrated screening validates primary axes of specialization in plants. *Oikos* 79: 259–281.
- Hairston NG Jr, Lampert W, Cáceres CE, Holtmeier CL, Weider LJ, Gaedke U, Fischer JM, Fox JA, Post DM. 1999. Rapid evolution revealed by dormant eggs. *Nature* 401: 446.
- Holt RD. 1993. Ecology at the mesoscale: The influence of regional processes on local communities. Pages 77–88 in Ricklefs R, Schluter D, eds. *Species Diversity in Ecological Communities*. Chicago: University of Chicago Press.
- Holt RD, Gaines MS. 1992. Analysis of adaptation in heterogeneous landscapes: Implications for the evolution of fundamental niches. *Evolutionary Ecology* 6: 433–447.
- Hooper DU, Vitousek PM. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277: 1302–1305.
- Jackson ML, Levelt TVM, Syers JK, Rex RW, Clayton RN, Sherman GD, Uehara G. 1971. Geomorphological relationships of tropospherically derived quartz in soils of the Hawaiian Islands. *Soil Science Society of America Journal* 35: 515–525.
- Janzen DH. 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* 7: 347–91.
- Jones CG, Ostfeld RS, Richard MP, Schaubert EM, Wolff JO. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* 279: 1023–1026.
- Jordan WR III, Gilpin ME, Aber JD, eds. 1987. *Restoration Ecology*. Cambridge (UK): Cambridge University Press.
- Lee C–K, Klopp RG, Weindruch R, Prolla TA. 1999. Gene expression profile of aging and its retardation by caloric restriction. *Science* 285: 2390–2393.
- Levine JM, D'Antonio CM. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* 87: 15–26.
- Naeem S, Li S. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390: 507–509.
- Noy–Meir I. 1974. Desert ecosystems: Higher trophic levels. *Annual Review of Ecology and Systematics* 5: 195–214.
- Pellmyr O, Leebens–Mack J, Thompson JN. 1998. Herbivores and molecular clocks as tools in plant biogeography. *Biological Journal of the Linnean Society* 63: 367–378.
- Petchey OL, McPhearson PT, Casey TM, Morin PJ. 1999. Environmental warming alters food web structure and ecosystem function. *Nature* 402: 69–72.
- Pimm SL. 1989. Theories of predicting success and impact of introduced species. Pages 351–367 in Drake JA, DiCastrì F, Groves RH, Kruger FJ, Mooney HA, Rejmánek M, Williamson MH, eds. *Biological Invasions: A Global Perspective*. Chichester (UK): John Wiley & Sons.
- Polis GA, Holt RD, Menge BA, Winemiller K. 1996. Time, space and life history: Influences on food webs. Pages 435–460 in Polis GA, Winemiller K, eds. *Food Webs: Integration of Patterns and Dynamics*. New York: Chapman and Hall.
- Polis GA, Anderson W, Holt RD. 1997. Towards an integration of landscape ecology and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289–316.
- Polis GA, Hurd SD, Jackson CT, Sanchez–Piñero F. 1997. El Niño effects on the dynamics and control of a terrestrial island ecosystem in the Gulf of California. *Ecology* 78: 1884–1897.
- Power ME, Rainey WE. In press. Food webs and resource sheds: Towards spatially delimiting trophic interactions. In Hutchings MJ, John EA, eds. *Ecological Consequences of Habitat Heterogeneity*. London: Blackwell Scientific.
- Rejmánek M. 1989. Invasibility of plant communities. Pages 369–388 in Drake JA, DiCastrì F, Groves RH, Kruger FJ, Mooney HA, Rejmánek M, Williamson MH, eds. *Biological Invasions: A Global Perspective*. Chichester (UK): John Wiley & Sons.
- Rejmánek M, Richardson DM. 1996. What attributes make some plant species more invasive? *Ecology* 77: 1655–1661.
- Ritchie M, Olff H. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400: 557–560.
- Rosenzweig ML. 1995. *Species diversity in space and time*. Cambridge (UK): Cambridge University Press.
- Sears A, Holt RD, Polis GA. In press. The effects of temporal variability in productivity on food webs and communities. In Polis GA, Power ME, Huxelm G, eds. *Food Webs at the Landscape Level*. Chicago: University of Chicago Press.
- Simberloff D, Schmitz DC, Brown TC, eds. 1997. *Strangers in Paradise: Impact of Management of Nonindigenous Species in Florida*. Washington (DC): Island Press.
- Sterner RW. 1995. Elemental stoichiometry of species in ecosystems. Pages 240–252 in Jones CG, Lawton JH, eds. *Linking Species and Ecosystems*. New York: Chapman and Hall.
- Thompson JN. 1998. Rapid evolution as an ecological process. *Trends in Ecology and Evolution* 13: 329–332.
- _____. 1999. The evolution of species interactions. *Science* 284: 2116–2118.
- Thompson JN, Cunningham BM, Segraves KA, Althoff DM, Wagner D. 1997. Plant polyploidy and insect/plant interactions. *American Naturalist* 150: 730–743.
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300–1302.
- Vitousek PM, Hooper DU. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. Pages 3–14 in Schulze E–D, Mooney HA, eds. *Biodiversity and Ecosystem Function*. Berlin: Springer-Verlag.
- Wall Freckman D, Blackburn TH, Brussaard L, Hutchings P, Palmer MA, Snelgrove PVR. 1997. Linking biodiversity and ecosystem functioning of soils and sediments. *Ambio* 26: 556–562.
- Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: An example from rain forest trees. *American Naturalist* 156: 145–156.
- Weihner E, Keddy P, eds. 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. New York: Cambridge University Press.
- Whitham TG, Martinsen GD, Floate KD, Dungey HS, Potts BM, Keim P. 1999. Plant hybrid zones affect biodiversity: Tools for a genetic-based understanding of community structure. *Ecology* 80: 416–428.
- Wilson JB. 1999. Guilds, functional types and ecological groups. *Oikos* 86: 507–522.