

**FRONTIERS OF ECOLOGY:
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INTRODUCTION

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 the major ecological questions faced by our society.

The Frontiers of Ecology workshop evaluated 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. In the end we distilled the discussion into four specific frontiers in research on the ecological structure and dynamics of the earth's biological diversity. Our report summarizes those frontiers and why they are crucial to our understanding of how ecological processes shape the constantly changing patterns of global biocomplexity.

FOUR MAJOR RESEARCH FRONTIERS

Each of the four major research frontiers takes a different approach to the overall ecological dynamics of biocomplexity. All require integration and collaboration among research approaches. These overlapping frontiers themselves are not new. Within each frontier, however, are emerging questions and approaches that will help make it possible to 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 systems from a regional species pool, which depends on interactions among species availability, the physical environment, evolutionary history, and the temporal sequence of assembly. Despite a long history of study, ecologists still cannot predict the pathways or endpoints of community assembly with any degree of certainty. Much of what we know comes from a handful of easily-studied systems, making it difficult to generalize from one community to another. We cannot predict which species are likely to invade or be lost from particular natural communities. We also know little about community responses to perturbations at different stages in development. Many attempts to create or restore communities (e.g., freshwater-wetlands or salt marshes) fail, for reasons that remain poorly understood. Most of these efforts focus on macro-organisms, whereas the functioning of communities undoubtedly depends heavily on the little-studied "hidden players" such as microbes, fungi, and soil invertebrates. Given these fundamental gaps in our knowledge, human impacts on community patterns will remain hard to predict.

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. Experimental efforts to understand the functional

relationships within constructed communities are in their infancy, but they hold great promise as tools. In the process, we are faced with the problem of the poorly known systematics of many smaller or cryptic organisms, which may form functional groups crucial for our understanding of community coalescence. The difficulty of linking important ecosystem functions to key players, hidden or not, is a particular challenge.

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

Functional traits and community composition. We do not know which traits of species are most important in determining the probability of invasion or extinction within developing communities. The importance of these traits may depend upon community context (existing species composition and historical development) at any point in time. We do not know whether coevolved species or local populations differ from coevolutionarily naïve populations in the strength or nature of their interactions during or after community assembly. Furthermore, we lack an understanding of how historical events and critical thresholds (species richness, functional group composition) interact with particular traits to facilitate assemblage persistence or maintain levels of key functions or processes.

Pathways toward community coalescence. For any pool of potential community members there is an enormous number of possible assembly sequences and endpoints. This is less of a problem if many of the alternative pathways tend to converge on a limited subset of endpoints. To that end, we need know whether developing communities move toward single or multiple points or states (attractors). Any such tendencies may vary through the course of community development. 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 potentially limit pathways of community development by changing the physico-chemical environment and altering biogeochemical cycles. Global homogenization of the species pool may itself alter pathways or endpoints of community assembly.

Functional groups. Ecologists recognize that functional groups provide a valuable tool for simplifying community complexity to manageable levels. Currently, most groups are defined in an ad hoc system-specific way, based upon biochemical, morphological, or trophic criteria. These criteria, however, do not work equally well for all groups. We need to develop a general framework defining and objectively identifying functional groups. The impact of functional group structure on assembly dynamics is also uncertain. We do not yet understand 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). Process-level feedbacks need to be considered as important drivers of community assembly.

Hidden players. Community assembly almost certainly depends upon hidden players (e.g., microbes, soil microfauna, mutualistic symbioses) that have historically been ignored or unrecognized through technological limitations and biases in the training

of ecologists. These ecologically cryptic species may play a keystone role in community development and function, and their absence may be responsible for failed attempts at community restoration. The importance of these hidden players may often become apparent only when they become problems, as sometimes happens when we alter community structure. Lyme disease may be an example of the emergence of a hidden player in response to changes in community composition and landscape patterns. 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., old-fields, temperate lakes, rocky intertidal shores). Study of under-represented communities, taxa, and interactions may 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. 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. That, in short, is 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. We lack that understanding, yet our societies are moving forward quickly in attempts to manipulate community assemblages worldwide. A more comprehensive theory of community coalescence is needed if we are to succeed in efforts to mitigate the effects of invasive species on local communities and make those communities less prone to extinction. Deliberate introduction of species, as occurs now in biological control efforts, will surely be less risky if we understand how control of species can be enhanced through the assembly of persistent but self-limiting subwebs. Similarly, bioremediation efforts would benefit from a better understanding of how we can develop persistent self-limiting assemblages of species that accumulate or degrade toxic wastes.

Research Frontier 2: Evolutionary and Historical Determinants of Ecological Processes: The Role of Ecological Memory

The dynamics of community coalescence outlined in Frontier 1 are continually shaped by a combination of the genetic and evolutionary structure of organisms and the recent history of past environmental events. Biology is a science strongly influenced by historical events. Unlike much of physics or chemistry, one cannot predict what happens at time $t + 1$ by knowing only the conditions at time t . Evolution and environmental history impose "ecological memory" on communities, introduce time lags in ecological processes, and constrain the trajectories of community composition in ways that are poorly understood. The ecological memory is encoded in the genetic structure of species and the current structure of biological communities. It affects how communities assemble, and it may 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 it is common among biologists to 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. Six crucial problems need to be addressed 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? As a result of shared phylogenetic history, species cannot be treated as independent units in their ecological roles. We know, for example, that ecological specialization is strongly phylogenetically constrained. Nevertheless, few studies have analyzed how shared species' traits and historical biogeography combine to constrain and shape community and ecosystem structure. There is a clear need to integrate phylogenetic non-independence into community and ecosystem ecology.

Rapid evolution and ecological dynamics. To what extent are succession, population dynamics, and ecosystem dynamics, historically considered as solely ecological processes, governed by rapid evolutionary change in species and their interactions? For example, some studies in successional fields have shown the distribution of nitrogen-fixing clover genotypes changes across landscapes during succession as a result of associations with different arrays of species. Such changes may subsequently influence nitrogen cycling in these communities. Similarly, 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 in response to eutrophication. There are now dozens of examples in which ecologically important traits of species are known to have evolved during the past century.

Coevolution and ecological dynamics. How does the history of species co-occurrence 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 co-occurred. These techniques could provide us with the ability to determine if populations, species, and communities that share a history of co-occurrence exhibit different properties from those created largely from recent invasions or restoration efforts. We need to know if 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? We need to understand the spatial scale at which ongoing evolution and coevolution shape 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. Both natural and anthropogenic

fragmentation of populations restricts the exchange of individuals among communities both historically and currently. Nevertheless, we know little about 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. This lack of understanding is becoming a more acute problem as we attempt 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? No studies have truly integrated the effects of genetic diversity *per se* into the temporal dynamics of ecosystem structure and function. The study of plant hybrid zones has given a glimpse of the potential far-reaching effects of the structure of genetic diversity on community dynamics. Hybrids of some species are much more susceptible to herbivores than are either of the parental species. Moreover, some hybrids support greater diversity and biomass of insect herbivores, birds, and other species, thereby becoming local foci of diversity.

Genomics of ecological dynamics. How do genomic content and patterns of gene expression shape species distributions, species interactions, and responses to changing environments? We know little about how something as fundamental as chromosome number shapes large-scale patterns in community structure and dynamics. Yet, chromosome number is tied to ecologically important attributes of taxa such as species distributions (e.g., proportion of polyploid plant species increases with latitude), invasiveness (possibly in some pines), and susceptibility of plants to herbivores (moths on saxifrages).

The role of environmental history and temporal variability. Ecological research needs a better integration of scientists working at 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 events or processes that occurred in the past. Three components of environmental history and temporal variability appear to be particularly important in shaping community dynamics. These include 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 vary through time at different scales, shaping species composition in the short-term (e.g., during recent invasion), medium-term (population expansion, range contraction), and long-term (historical biogeography).

Historical variability in productivity/resource input. Resources vary in availability over time in all communities through abiotic (e.g., wet vs. dry seasons; El Niño vs. La Niña years) and biotic influences (mast years in trees, pig wastes flowing into watersheds). Such variation has been characterized ad hoc by ecologists working on particular taxa or communities. Nevertheless, no coherent body of theory addresses how past periodic or pulsed productivity affects the dynamics of populations, consumer-resource interactions, food webs, communities, and ecosystems. We need to achieve a

synthetic understanding that integrates theory with empirical work to produce a conceptual framework of how temporally variable productivity influences food web processes, community dynamics, and ecosystem function. For example, El Niño rains (La Niña drought) may stimulate or depress terrestrial productivity, thereby allowing subsequently high or low abundances of consumers and altering consumer-resource interactions. On smaller spatial scales, the pattern of local competitive outcomes in forests may depend upon the pattern of tree falls and old allelopathic footprints, both of which may produce long-lasting changes in local soil chemistry.

Historical variability in species composition, abundance, and interaction strength. We require a better understanding of how past community configurations shape current processes. For example, we have little understanding of how bird extinctions over the past few hundred years – including dodos and passenger pigeons – have altered communities and whether those extinctions are still affecting the dynamics of communities today. We do know that new introductions of species depend upon past presence of particular taxa. Introduction of cows into the Intermountain West of North America led to very different effects on grassland and steppe communities than introductions east of the Rockies due to differences in the past history of association of these grasslands with bison. 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 their presence is not interpretable from analysis of current ecological conditions or their recent life history statistics (e.g., measurement of intrinsic rate of natural increase).

Historical variability in key abiotic events. Erratic large scale disturbance regimes leave ecological legacies or propagate historical echoes. Volcanoes, hurricanes, El Niño storms, or changes in Antarctic anchor ice all reshape biological communities in ways that have long-lasting effects. We cannot understand the present without knowledge that these events occurred in the past. Moreover, we do not have a full appreciation of which of these major periodic environmental changes are the most important in shaping global patterns in ecological processes.

Research Frontier 3: Emergent Properties of Complex Systems: Biophysical Constraints and Evolutionary Attractors

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

Phenotypic traits are products of adaptive evolution operating within bounds set by physical and chemical constraints. Physiological and functional ecology have explored how these constraints affect the anatomy, morphology, and behavior of individual species. Today, an important frontier is to expand 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 behavior (ecosystem function), and

anatomy (physiognomy) 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.

We can imagine a community to be a set of species plotted in multi-dimensional phenotypic space. Enclosing this space is a set of boundaries and constraints that derive from basic energy and thermodynamic principles. For example, we know that matter devoted to one use is unavailable for other uses. Such biophysical constraints generate some of the tradeoffs in evolution. Within these bounds, selection tends to maximize fitness. Using a term from dynamic systems theory, the result is an attractor, defined as 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 dynamical system of organism and environment, where the organism attempts to maximize its fitness in the face of 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 area. Material and energy fluxes for competing species and consumers of that plant may then, in turn, be altered.

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 increases as the 0.75 power of body mass. Although there has been turnover of species along this curve over time, the physical basis of this power law insures that the curve itself has remained fixed. Such an evolutionary attractor works by a combination of physical principles and evolutionary optimization. Phenotypes that deviate from this attractor are at a significant disadvantage compared to those near the attractor.

Biochemical constraints may also result in an evolutionary attractor on life history evolution. Ecological stoichiometry considers patterns in element concentration among different species. Work in that field has indicated that for a species to have rapid biomass growth it must have an element composition with relatively high phosphorus composition, a result of the element composition of anabolic biochemical machinery (in particular, ribosomes). 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 reliance on carbon (for wood) or calcium

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. The questions we need to answer on the physical basis of evolutionary attractors include 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 upon 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 be extrapolated to predictions or estimates of diversity?

A barrier to successfully crossing this frontier will be to find means to perform rigorous experimental tests, or other ways to test hypotheses. Multi-species 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 fastest to reproduce) organisms, but microbial taxa make excellent experimental tools for some of these questions. For most other taxa, less direct means of testing mechanistic hypotheses will be necessary.

New techniques. This highly integrated view of evolution and ecosystems can be aided by the new approaches in the study of structural and functional genomics. 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 possible for ecologists to study the relationships between biophysical constraints and evolutionary attractors. For example, recent studies have described the patterns of expression of 6347 genes in mice raised under caloric restriction. Caloric restriction retarded aging by causing a metabolic shift toward increased protein turnover and decreased macromolecular damage. These experiments provide a glimpse at 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 probe how species' genomes mutually 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: Defining the Spatio-Temporal Domains of Causality for Ecological Structure and Process.

Frontiers 1 through 3 all require that we reevaluate the scale of ecological processes and the analytical methods by which we study them. We need a way of determining how best to incorporate the combined effects of space and time acting at different scales—an ecological topology. We can think of this ecological topology as a set of domains of causality. Ecologists have long been concerned with delimiting communities or ecosystems in ways that provide dynamical sufficiency. For instance, what are the factors that control rates of primary production by native plants on Mauna Loa in Hawaii? The most important controls may be local to Mauna Loa, regional through the impact of introduced plants and animals throughout the island, or even broader, set by phosphorus in aeolian dust blown in from Central Asia that was mobilized by agricultural practices starting during the Han Dynasty in the 3rd to 4th century B.C. The appropriate domains of causality in many ecological studies could extend far beyond previously assumed spatial and temporal bounds.

We therefore need a unified way of incorporating 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 problems such as the structure of food webs generally lacks a spatio-temporal context, which strongly limits our ability to explain their origin, maintenance, or consequences. We suggest building an ecological topology that addresses these needs. Ensuring dynamical sufficiency in our explanatory models requires much more than delimiting physical boundaries. It requires characterizing patterns of movement of individuals and flow of materials across space and through time. 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 local scale to larger ones.

We now have, or could soon develop, the tools to investigate and characterize the bounds of such spatio-temporal domains. Genetic and isotopic tracers are increasingly available for following the movement of matter and organisms. 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. We highlight a few of these here:

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 understand just how far we should routinely expand the domains of our search if we are to interpret correctly ecological patterns and processes.

Identifying the rules. What rules govern the origin and maintenance of ecological topologies—those that function adequately, or optimally (if subject to thermodynamic or evolutionary selection) to solve problems? Clearly, there are some general rules governing the geometries of circulatory systems, or the drainage networks of watersheds. This is an active area of research in scientific fields outside ecology that could inform us about feasible bounds on causal domains set by whole system constraints—a valuable theoretical supplement to ecologists' efforts to delineate them in an empirical, LaGrangian fashion by following movements and reconstructing histories of component entities.

Changing the bounds. How will ecological systems 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 re-arrangement of nature ever attempted. Interbasin water transfers are now common throughout many arid regions of the world, depleting or artificially augmenting local ecosystems and ground water 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. This has occurred, for example, as we have begun to replace wild-caught populations of salmonids that harvested huge areas of ocean production with cage-cultured fish that feed only in the mouths of estuaries. It is worth exploring whether causality domain theory can give us an improved ability to predict the longer-term consequences of ecological distortions of various types and magnitudes.

Focus on these ecological topologies would require a change in how ecologists typically think of ecosystems. In most conventional uses, the term "ecosystem" refers to a particular contiguous unit of the landscape. The system is defined with inputs and outputs, and internal dynamics. Most management practices similarly focus on ecological processes and patterns defined by habitat units such as this. Nevertheless, many if not most ecological processes can be envisaged as being caused by a set of rules, each of which operates over a unique spatial and temporal scale. We would gain a great deal by coming to understand the topology of these spatio-temporal domains.

MEETING THE CHALLENGE

Collaboration and integration. No single scientist can develop the depth needed across all the physical and biological sciences to address the questions at the frontiers. Instead, we must foster increased research collaborations among scientists who are trained to understand the language of one another. Meeting that challenge will require renewed effort to train ecologists 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 are needed across all the frontiers. Despite the formation of departments of ecology and evolutionary biology throughout the U.S. during the past thirty years, there remains a major gap between these disciplines. Only a small proportion of ecologists has ever had a formal course in evolutionary processes, and only a very small proportion has ever had advanced training in evolutionary theory and methods. Similarly, a large proportion of evolutionary biologists have very little advanced training in current ecological theory and methods. Incorporating an evolutionary framework into ecological research requires explicit training of scientists well versed in both ecological and evolutionary theory.

Analogously, there is a need to strengthen the links between ecosystem and community ecology. Significant advancement will occur as the various barriers break down between these two complementary, but traditionally separate, subdisciplines of ecology.

Analytical tools. The mathematical and statistical constructs used in ecological research come mostly from linear theory. In contrast, many ecological processes are governed by non-linear dynamics, threshold effects, and more complex relational structures. We need a renewed emphasis upon ecological theory that builds upon the structure of empirical results in ecology. Meeting this goal will require the training of a generation of empirical ecologists with much stronger quantitative skills and theoretical ecologists with a detailed understanding of the empirical structure of ecological processes.

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 remains a major hurdle in ecological analysis. The experience of dozens of working groups at NCEAS has highlighted this need as they try to summarize and compare data collected over decades for a wide variety of purposes. 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 only useful for ecological analyses if their results are readily accessible to ecologists everywhere.

Moreover, to work with diverse data sets, we need to standardize collection methods and data entry methods 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 to studies within subdisciplines and attempt standardization where possible.

The hidden players. Our understanding of microbial ecology is rapidly advancing, but it faces daunting hurdles. These hidden players include a vast array of free-living species, parasites, and participants in mutualistic symbioses. But most microbial species are simply unknown and cannot be cultured. Consequently, we cannot yet begin to address many of the most fundamental questions of how microbial diversity contributes to the dynamics of biocomplexity. Moreover, it is not yet clear how the structure of microbial diversity should be incorporated into many kinds of analysis of the local, regional, and global dynamics of ecological processes. Traditional definitions of species and traditional metrics of distribution and abundance are often a poor fit to the structure of microbial populations and communities.

The need for stronger links between systematics and ecology is evident for all taxa, but it is especially critical now for microbial groups. We must train 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.

CONCLUDING REMARKS

There is no question that ecological research is entering a new era. Each of the frontiers requires increased collaboration and technology if we are to understand how the complexity of ecological processes continues to reshape the earth. Unlike many scientific disciplines, most central problems in ecology involve understanding how biological and physical processes interact over multiple spatial and temporal scales. Those central problems permeate the four interrelated research frontiers we have identified. Crossing the frontiers will demand strong cross-disciplinary training and collaboration, coordination of observational and experimental approaches across large scales, incorporation of new technologies, and increased access to the growing database of ecological results.