

# Frontiers in Evolutionary Biology

REPORT OF A WORKSHOP

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## INTRODUCTION

Support for ecological and evolutionary research at the National Science Foundation expanded substantially during the past decade. To help guide this expansion, in October 1998 the Population Biology program at NSF hosted a workshop on “Frontiers in Population Biology”. The report from that workshop identified and illustrated seven research themes of special interest in population biology, and described how these themes connect to genetics/genomics on the one hand and to environmental issues on the other. The report has been valuable to officers at NSF in shaping their programs and balancing their grant portfolios.

Our understanding of evolutionary biology has advanced enormously in the past six years. The explosion of genomic information, rapid advances in computer and sensor technology, and the development of sophisticated new statistical and analytical approaches coupled with the recent reorganization of programs at NSF make this an appropriate time to evaluate progress and to identify areas in which new investment is warranted. In January 2005 a panel of experts met at NSF to identify areas that represent the frontiers for evolutionary research in the coming decade. The scope of this workshop was somewhat larger than that considered at the 1998 workshop, reflecting the range of evolutionary research and topics considered by Population and Evolutionary Processes, Ecological and Evolutionary Physiology, Animal Behavior and related programs at NSF. In addition to identifying nine thematic areas within evolutionary biology, the panel considered how questions within these areas relate to questions in molecular genetics and genomics, systematics, environmental sciences and other areas.

In reflecting on research frontiers that have emerged since 1998, two related trends are evident. First, evolutionary approaches and perspectives are increasingly an integral part of all areas of biological research, from molecular biology to macroecology. As a result, we are increasingly able to explore the mechanisms, processes and patterns of evolutionary change at multiple levels of biological organization from the gene to the ecosystem. Second, technological advances in genomics, computation, and informatics have provided a world of new tools and information to apply to evolutionary questions. These and similar technical advances will continue to be a key factor in pushing the

frontiers of evolutionary research in the coming decade. As a result, the themes for future research outlined here reflect both new questions and new conceptual frameworks, as well as the application of new tools to classic questions in evolutionary biology.

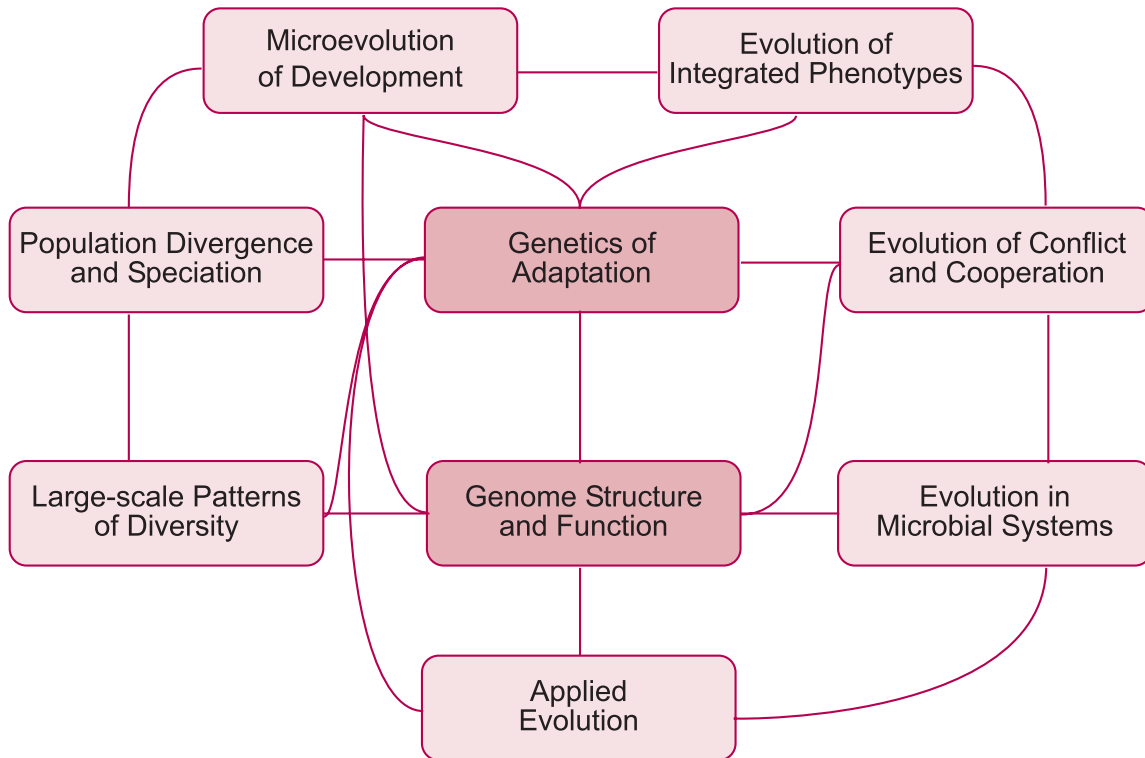
The workshop had four specific goals:

- 1) To identify **emerging tools** essential to evolutionary research;
- 2) To identify and illustrate **research themes** of particular promise;
- 3) To summarize major **institutional resources** available to support evolutionary research;
- 4) To suggest **infrastructural needs** and opportunities for enabling the next generation of advances in our understanding of evolution.

## EMERGING TOOLS

Many research frontiers identified in this report are now accessible only because of recent, explosive advances in technology, while others lie at the fringe of current technology. A shared feature of many of these advances is the scale at which they are conducted. We can now sequence whole genomes, analyze expression of all genes, and analyze data with desktop supercomputers. It is clear that advances in phenotypic analysis equivalent to those on the genomic and computational side are needed, as these research frontiers require a variety of high-throughput, high-precision techniques for measurement of genetic, physiological, and phenotypic characteristics in large numbers of individuals in the field as well as in controlled, laboratory environments.

- **Genomics** – The advent of high throughput DNA sequencing has led to the availability of whole genome sequences for a broad phylogenetic sample of organisms, including replicate genome sequences for different individuals of the same species. Microarray analyses of gene expression (and similar methods) allow dissection of complex genetic networks involved in physiological, developmental, and behavioral responses. Large-scale genetic manipulation allows experimental tests of adaptive hypotheses involving particular genes or sets of genes. Environmental DNA provides insights into the physiological and evolutionary dynamics of unculturable microbes. **Challenge:** to



**Figure 1:** Connections among research frontiers identified in this report.

- connect sequence-and expression-level data with organismal phenotypes and responses.
- **Analytics** – The high-speed computational resources now available enable complex statistical analyses and simulation studies faithfully reflecting details of biology that were previously impossible. Genome, phylogenetic, and environmental databases provide a wealth of information about the genetic characteristics of organisms, their evolutionary relationships, and the external environment in which they occur. Continued statistical and computational developments are paving the way for a reconciliation of historical and cross-sectional analysis of genetic variation. **Challenge:** to develop the conceptual framework for large-scale databases of organismal phenotypes, the tools necessary to integrate these disparate databases into a comprehensive resource for analysis of large-scale patterns in genomic and phenotypic evolution, and the statistical techniques for fine-scale evolutionary analysis of population history.
  - **Phenomics** – Advances in sensor technology enable real-time measurements of many important physiological variables in the field. Advances in sensor design will

allow them to record corresponding environmental variables at the scale at which organisms sense the environment. Wireless technologies allow these measurements to be recorded without capturing or relocating the individuals, and future integration with global positioning systems will allow these data to be integrated with fine-scale climate and environmental variables. **Challenge:** to develop high-throughput methods allowing complex phenotypic measurements to be made reproducibly at high frequency on a large number of individuals.

## RESEARCH THEMES

Research questions in evolutionary biology are highly interrelated. Answering fundamental questions about organismal adaptation, for example, requires understanding not only the consistency, magnitude, and objects of natural selection but the ways in which genome structure (including the structure of gene regulatory networks) influences the distribution of mutational effects and the response to selection. Moreover, determining how genome structure influences the evolution of integrated phenotypes is vital if we are to understand how individual-

level differences in development are related to mechanisms of species divergence and large-scale patterns of biotic diversity.

The workshop identified nine interrelated themes as research frontiers, broad areas where existing or foreseeable technology makes great advances possible in the next decade (Figure 1).

### **The Evolution of Genome Structure and Function**

**Scope:** Evolutionary change requires change in the architecture or components of genomes, and organismal properties determined by genetic or molecular interaction networks that arise from the expression of genes. Understanding genomes, their components, and the interaction networks that arise from them is fundamental to a modern understanding of the genetic basis of evolutionary change.

**Rationale:** Genomes are highly complex molecular assemblages that encompass the fundamental physical organization of genetic information in organisms. Fundamentally, genomes are organized to encode the genetic information in discrete units (genes) as well as to contain sequence elements (e.g., centromeres and telomeres in most eukaryotic systems, *ori* sequences in bacteria) necessary for the transmission and maintenance of genetic information.

Genomes also have specific architectures and components that vary dynamically both within and among species. We are beginning to understand that single-gene approaches to understanding genome structure and function are insufficient. Individual gene products are embedded in large-scale interaction networks that represent integrated functional units at the molecular genetic level.

Our understanding of the evolutionary dynamics of diversification in genome structures and their associated molecular genetic networks, however, remains limited. Moreover, few comparative genomic studies are underpinned by a clear phylogenetic context. Finally, we lack theoretical analyses to inform our understanding of how genomes and their associated genetic networks evolve. The revolution in genomics technologies and resources, including whole genome sequences, low-cost sequencing, microarray technologies and computational power, now allow us to begin to address questions surrounding the evolution of genome structure and function.

#### **Frontier questions**

- What are the extents and rates of changes in genome structure and size, and what are their functional consequences for organismal evolution?
- How do new genes arise and go extinct?
- How does selection act on large-scale variation in genome structure and organization?
- What are the relative roles of changes in structural, regulatory, and non-genic sequences in organismal evolution?
- What evolutionary forces determine transposable element activity and number in genomes, and what are the functional consequences of these mobile elements?
- What is the structure of genetic networks, how do they evolve and how does network topology influence organismal evolution?
- What are the evolutionary causes of differences in recombination and mutation rates across the genome?

### **Genetics/evolution of adaptation**

**Scope:** Adaptation requires both that organisms differ in fitness and that those fitness differences be heritable. Understanding how adaptive traits evolve requires that we integrate genetic analyses of phenotypic differences with analyses of the performance consequences of phenotypic differences in an ecological context.

**Rationale:** Molecular genetic studies have provided a wealth of information on historical patterns and rates of evolution of particular genes but have rarely made a connection with particular phenotypes or adaptive value. Similarly, a great deal is known about the adaptive value of specific phenotypes in ecological contexts and rates of phenotypic evolution, but little is known about their genetic basis. While connecting these types of studies has been an underlying goal in evolutionary biology since the synthesis of evolutionary theory and genetics, only now has it become possible to make these connections explicit. New genomic, molecular and computational tools offer the opportunity to link genetic variation at the DNA level with phenotypes, even in non-model organisms. Combined with technological advances and novel theoretical machinery, we now have an unparalleled ability to measure selection on the genes underlying phenotypic variation in natural populations. Furthermore, improved understanding of gene functions and interactions will allow us to study more fully the evolution of adaptive phenotypes. Investigations

into the existence of generalities concerning the genetic basis of adaptive evolution will require studies in many different organisms over long periods of time.

#### **Frontier questions**

- What is the molecular basis of adaptation?
- What types of genes are involved in adaptation: regulatory or structural?
- What types of mutations are involved in adaptation: non-coding, point, indel, transposable elements?
- What genetic features of adaptive evolution are convergent?
- To what extent is phenotypic convergence the result of genetic convergence?
- How can an understanding of the molecular bases of adaptation reveal historical patterns of adaptation in natural populations?

#### **Population divergence and speciation**

**Scope:** Population divergence and speciation are fundamental processes for the generation of biological diversity. They produce the boundaries within which microevolutionary forces act. They are manifest by changes in the allelic composition of phenotypic variation among both diverging populations within species and recently diverged species groups.

**Rationale:** New approaches and technologies are facilitating unprecedented insights into the mechanisms of population divergence and speciation. The ability to apply these technologies to non-model systems offers the opportunity to probe a diversity of speciation patterns and mechanisms. This comparative frontier will enable syntheses of evolutionary forces that cause phenotypic divergence and speciation, an understanding of genetic architectures of diverging traits and populations, and predictions about the extent and direction of possible gene flow between species. Phenotypes of particular interest include those underlying prezygotic incompatibility, such as morphological and behavioral traits involving sexual or ecological isolation, and those underlying postzygotic incompatibility, such as developmental or physiological traits causing hybrid sterility or inviability. Understanding how these traits evolve requires that we understand the distribution of genetic variation within and among diverging species, the shape and topologies of gene genealogies that give historical insight into that genetic variation, genome and chromosomal structural variation between recently formed species, and the genetic

architecture of traits that differentiate populations and species.

#### **Frontier questions**

- How do gene-genealogies diverge at speciation?
- What is the genetic architecture of behavioral, ecological, physiological and developmental incompatibilities that cause reproductive isolation? How does genetic architecture constrain or promote divergent selection on such traits?
- Do pre-zygotic incompatibilities evolve more frequently or less frequently than post-zygotic incompatibilities in the initial stages of divergence?
- What proportion of the species' genome is impervious to gene flow? What are the consequences of porous species boundaries? What is the role of hybridization and genome reorganization in speciation?
- Must gene flow be absent for speciation to occur? How common are the conditions under which sympatric speciation can occur? How common is reinforcement?
- Is the standing genetic variation within species the major genetic reservoir for speciation?
- What can the patterns of variation among taxa tell us about the evolutionary processes by which they arise?

#### **Microevolution of development**

**Scope:** All phenotypes in multicellular organisms are the result of development. An emerging understanding of developmental mechanisms coupled with recently developed genomic tools makes it possible for the first time to study the evolutionary mechanisms by which differences in organismal development arise.

**Rationale:** The last twenty years of work in developmental genetics has generated detailed information regarding shared and divergent features of the developmental mechanisms that underlie phenotypic (primarily morphological) differences among broad taxonomic groups. These studies have revealed the surprising result that there is a shared set of developmental and regulatory processes (a shared "developmental toolbox") that serves as the foundation for development within plant and animal systems. How can we understand organismal diversity in the face of this apparent pattern of conservation? Armed with a better grasp of large scale *patterns* of the evolution of development, it is now appropriate to turn our attention more fully to the



evolutionary *processes* that lead to these patterns.

Rapid advances in the detailed analysis of developmental mechanisms within model taxa coupled with increasing availability of genomic and functional genomic information now allows for detailed studies of variation in developmental processes within populations. These studies include an analysis of molecular variation and molecular evolution of developmentally relevant loci, as well as variation in functionally related characters such as levels and localization of gene expression. Complementary to the study of variation within populations is the examination of divergence in developmental characters among closely related species. The increasing availability of genomes of closely related taxa will facilitate this work. Another exciting area of future research centers on placing this developmental information into an environmental and ecological context relevant to the whole organism.

#### **Frontier questions**

- How does phenotypic variation arise from variation during development? How does selection act on this variation?
- What are the developmental mechanisms underlying phenotypic differences among closely related species and how are these differences related to variation within-species?
- What is the level of natural variation in genes affecting different stages of development? What are the signatures of selection and drift on these genes?
- How do homologous developmental processes generate non-homologous phenotypes (i.e., what is the developmental basis of convergence and parallelism)?
- How does the structure of developmental pathways influence the evolution of the genetic components of those pathways?
- How is adaptive plasticity achieved through development modulation? What is the genetic architecture and molecular basis of plasticity?

#### **Evolution of Integrated Phenotypes**

**Scope:** Many diverse characteristics of an organism—morphology, physiology, behavior—combine to yield an integrated phenotype that determines its functioning in some set of environmental conditions. The phenotypic characteristics may range from gene expression profiles and metabolic fluxes to acoustic

signaling and locomotory performance, but understanding their evolution requires approaches that treat the phenotype as an integrated system rather than as a set of isolated traits.

**Rationale:** New approaches and technologies have enabled biologists to measure complex, integrated phenotypes and their functional consequences in increasing detail and sophistication. An individual's fitness is the result of an integrated suite of phenotypic traits interacting with environmental conditions; and many such traits are multi-dimensional functions of age and environmental conditions. However, evolutionary studies often characterize an individual's phenotype in terms of a small number of phenotypic traits, and consider variation and selection of phenotypes in a simple, atomistic manner. Recent technological advances make it possible to pursue a different approach, to understand variation and selection of integrated phenotypes and to investigate how this integration changes during evolution. An important related challenge is to develop the capacity to measure multiple components of integrated phenotypes on the large number of individuals required for lab and field studies of genetic variation, selection, and evolution.

#### **Frontier questions**

- What are the patterns of evolution in integrated suites of morphological, behavioral, physiological and other traits? Are there different patterns or rates of evolution for different types of traits?
- How do we visualize and quantify patterns of phenotypic and genetic variation in high-dimensional, integrated phenotypes?
- How modular are integrated phenotypes in a functional sense? How does functional integration emerge during development?
- How modular are integrated phenotypes during evolution? How readily are such modules co-opted into new functional roles during evolution?
- How do behavioral responses affect the pattern of selection on morphological, physiological and other traits? How do immune responses and behavior interact to influence their joint evolution?
- What are temporal and spatial patterns of selection on integrated phenotypes in natural populations? Are patterns of selection on integrated phenotypes different than for other traits?

- What are the genetic bases of phenotypic plasticity in integrated phenotypes? How do differences in the pattern and magnitude of plasticity affect selection and evolutionary responses?

### **Microbial Systems**

**Scope:** Evolutionary biologists have devoted relatively little attention to microbial and viral systems, even though microorganisms make up most of the tree of life. Both systems are particularly amenable to experimental evolution and to comparative genomics.

**Rationale:** New technologies that allow better sampling of both culturable and unculturable genomes have expanded the tree of life, uncovering a third domain, and have shown us the immense diversity in the microbial world. Evolutionary experiments using microbes or viruses have enriched our understanding of genetic change in novel environments, of host-pathogen evolution, and of the evolution of conflict and cooperation. Medicine, agriculture and industry are increasingly using evolutionary approaches to microbial and viral systems to interpret data, track pathogens, improve bioremediation, manage resistance, and design molecules and organisms for specific purposes. Microbial and viral systems are amenable to *in vivo* reconstruction of ancestral genes and their smaller genomes make them good candidates for evolutionary genomics. These systems also provide a new testing ground for theories developed for animals and plants, in which horizontal gene transfer may be much less important.

#### **Frontier questions**

- Are standard evolutionary models adequate to explain and predict microbial evolution? To what extent do results from experimental studies of microbes and viruses generalize?
- How do selection and co-evolution operate in structured microbial communities such as biofilms?
- What are the mechanisms and evolutionary consequences of horizontal gene flow? How does horizontal gene transfer influence cooperation and competition in microbial populations?
- What is the diversity of genome structure among microbes and viruses, and what is the functional significance of this diversity?
- How can we quantify microbial and viral diversity, define species, and classify unculturable organisms? How do microbial

lineages maintain species cohesion? Can we develop a species concept for microorganisms and viruses that captures their evolutionary history?

### **Evolution of conflict and cooperation**

**Scope:** Conflict is pervasive in the evolution of life, and it is the key element of many major transitions in the organization of life.

Evolutionary conflict occurs in interactions between species, between individuals, or between genetic elements, and is sometimes overcome by cooperation. Understanding how cooperation arises is important in explaining major transitions from the organization of genes in chromosomes, prokaryotes to eukaryotes, and other major transitions.

**Rationale:** Conflict and cooperation are crucial drivers of interactions within and between species. Between-species interactions include plant-fungus interactions, pollination, host-pathogen interactions, and ant-plant, or ant-fungus mutualisms. Selection operates on each partner to maximize their gain, and minimize their cost, which can lead to arms races and resulting rapid evolution.

Within species interactions include male-female interactions, worker-queen interactions, mother-fetus interactions and cell-cell interactions in chimeric organisms. Since the partners are members of the same species, selection for gain in one partner can favor genes that are detrimental when expressed in the other role, leading to overall evolutionary compromises in the organism. For example, genes for traits optimal in males make worse females.

What stabilizes these interactions, what allows cooperation to evolve in the face of selfish genetic interests, and how the signature of competition remains are questions that have only recently been made accessible by advances in genomics, phylogenetics, experimental evolution, and molecular manipulation.

#### **Frontier questions**

- What kinds of genes are important in social interactions?
- How prevalent is the role of imprinting in genomic conflicts?
- Is evolutionary conflict a major explanation for rapidly evolving genes? If so, what are the pleiotropic effects of rapid evolution?
- Are there general rules for the suppression of conflict during the evolution of cooperation? How are cooperating systems stabilized against cheaters?

- What determines the evolution of virulence? What is the genetic architecture of virulence?
- What is the role of evolution of conflict and cooperation in major evolutionary transitions such as the origins of multicellularity, endosymbiosis, and chromosomal organization?
- What is the role of sexual conflict in adaptation and speciation?

### **Large-Scale Patterns of Diversity in Time and Space**

**Scope:** Large-scale patterns of biodiversity, like the latitudinal species gradient and the diversity of communities, have not received satisfactory evolutionary explanations. Understanding the evolutionary basis for these patterns will require synthesis of within-population, microevolutionary studies with across-taxa, macroevolutionary investigations.

**Rationale:** The availability of well-corroborated phylogenies, data bases of species occurrences, and global environmental data now document the ecological and evolutionary scale of diversity at a large scale and in great detail, and the development of new conceptual approaches and computational methods permits analysis of these data in manners not previously possible.

Phylogenetic studies have become the standard means of investigating historical, comparative questions, and a plethora of analytical methods have been developed. At the same time, increasing understanding of past environments and biotas permits the synthesis of neontological and paleontological data in novel and mutually illuminating ways. Similarly, the recent development of coalescent and comparative phylogeographic methods for inference of within-species population histories now allows similar questions to be investigated at the level of among-population differentiation. As a result, it is now possible to investigate the relationship between processes leading to differentiation among populations of the same species and those leading to diversification of entire clades.

The challenge will be to develop methods that integrate across different disciplines and time-scales, spanning ecological, microevolutionary and macroevolutionary time. The assembly of suitable large scale data sets is vital. For example, the Tree-of-Life program is developing large-scale, highly resolved phylogenies for many groups of taxa; comparable efforts are needed to collect the data

on evolution of phenotypic attributes within these groups.

### **Frontier questions**

- Do different types of characters evolve at different rates and at different phylogenetic time scales within clades? Are there regular patterns of divergence for different types of phenotypic characters when compared across clades?
- How does the environmental niche of species evolve and to what extent is a species' range determined by adaptation to changing conditions? Does evolutionary change account for the success of invasive species, and can such change be predicted?
- How does the spatial structure of populations, species and communities affect evolutionary and coevolutionary change? How does the spatial structure of populations, species, and communities evolve?
- How can paleontological data be used to test neontological hypotheses of selection and divergence? How can neontological data test similar paleontological hypotheses?
- How are processes of within-species divergence related to diversification of clades?

### **Applied Evolution**

**Scope:** Applied evolution marshals our understanding of evolutionary principles to tackle significant environmental, epidemiological, and agricultural problems.

**Rationale:** The scale on which humans are changing the biosphere in the 21<sup>st</sup> century is unprecedented. Global pressures by humans on planetary resources not only cause extinctions and detectable shifts in species' geographic ranges and phenologies, but also cause measurable evolutionary change in natural and introduced populations. Emerging agricultural pests and pathogens are moved almost instantaneously around the globe. Applied evolution seeks ways in which evolutionary principles can improve the human condition. Its applications range from improving ecosystem services to developing better vaccines. It also encompasses a variety of approaches for determining the impact of human activities on rates and patterns of evolutionary processes. Finally, it includes efforts to trace the geographic and taxonomic origins of rapidly spreading pathogens, to better understand their biological effects and predict further spread, and to devise means of control.

Examples of applied evolution span the entire breadth of evolutionary biology. Using the tools of DNA sequencing and phylogenetics, evolutionary biologists can determine the time and geographic location of origin of invasive species and emerging diseases. Evolutionary principles can be used to develop enzymes, ribozymes, and even organisms with specific functions and catalytic properties. Population genetics and ecological modeling can help predict if and how readily genes in genetically modified organisms will spread into other organisms.

One major challenge in this field is to better predict the course of evolution given detailed information on the genetics and behavior of organisms. This aspect of applied evolution will have its greatest successes in understanding responses of very simple systems, such as those in microbes or viruses. In many cases, these same systems will be the ones with the greatest impact on human populations and environmental change.

Basic research has much to offer here. Experimental evolutionary approaches, in which evolutionary changes in laboratory populations are measured in real time, will play an important role in understanding the diversity of genetic and phenotypic responses to intense selection. By providing biologists with a catalog of genes and physiological properties, whole genome sequences of microbes and simple eukaryotes will also be a major bulwark of applied evolution in the future. Finally, large-scale monitoring of environmental variables, such as those envisioned in NEON, will allow biologists to predict with increasing certainty the spread and fate of organisms and pathogens and their impact on agriculture and the environment.

#### *Frontier questions*

- Are there rules to predict changes in virulence or resistant of pathogens? Can we predict potential pest/pathogen status based on ecological, genomic or phylogenetic characteristics?
- Can we use evolutionary theory to improve the efficacy of directed evolution? Conversely, can directed/experimental evolution inform evolutionary theory?
- Can we predict changes in selection and drift from changes in environmental conditions?
- Can we predict the relative frequencies of range shift, adaptation or extinction in response to environment change?

- What is the impact of the agricultural landscape on evolution of natural populations?
- What factors influence the extent and consequences of gene flow between GM crops and natural populations?

## INSTITUTIONAL RESOURCES

Many of the resources necessary to advance the frontiers of evolutionary biology are already in place. Others are only now coming into existence. Some of the resources needed are institutional, but the scale of some questions will require more collaboration among individual investigators than has been typical of evolutionary research in the past.

- *NEScEnt* – The National Evolutionary Synthesis Center will serve as a focal point for a variety of activities including databasing and informatics development, catalysis of cross-disciplinary interactions, and scientific synthesis. It will provide a venue for the assembly, annotation, and integration of major evolutionary databases, including genomic, phylogenetic, and phenotypic databases; for fostering the development of integrative, cross-disciplinary approaches to the solution of evolutionary questions; and for encouraging the integration and synthetic interpretation of evolutionary data and ideas.
- *NEON* – The National Ecological Observatory Network will provide an integrated, national platform at which a core set of standardized ecological variables is measured. It will provide a natural set of locations for large-scale experiments designed both to measure the strength, variability, and predictability of selection and to assess the influence of evolutionary history on large-scale community and ecosystem processes.
- *RCN* – Research Collaboration Networks, which had just been established at the time of the 1998 Working Group report, allow groups of individual investigators investigating similar questions to coordinate their research. Investigators who take advantage of the RCN program will be able to address more comprehensive questions than they could working in isolation from one another.

- **FIBR** – The Frontiers in Integrative Biological Research program encourages investigators to study “major, under-studied or unanswered questions in biology and to use innovative approaches to address them by integrating the scientific concepts and research tools from across disciplines including biology, math and the physical sciences, engineering, social sciences and the information sciences.” Many of the research frontiers identified in this report are natural candidates for support from the FIBR program.
- **IGERT** – The Integrative Graduate Education and Research Traineeship program “is intended to catalyze a cultural change in graduate education ... by establishing innovative new models for graduate education and training.” Many of the research frontiers in this report require integration of traditional biological disciplines with the development of new computational, statistical, and analytical tools. Graduate training programs that seek to train such students are natural candidates for support from the IGERT program.

## INFRASTRUCTURAL NEEDS AND OPPORTUNITIES

Much of the infrastructure required for advancing evolutionary research is already in place, as outlined above. There are, however, several areas in which the infrastructure falls short and which are vital areas for future investment.

- **Genomic resources:** The choice and development of genomic data and tools to date have naturally focused on genetic model systems and species of applied biomedical or agricultural importance. However, species vary in their utility for informing us about evolutionary patterns and processes. *Mus musculus*, *Drosophila melanogaster*, *Arabidopsis thaliana* and other species for which extensive genomic resources are now available allow us to answer some evolutionary questions and their full value is yet to be exploited, but these species are too divergent from one another and represent too little evolutionary diversity to allow us to answer many critical questions in evolutionary biology. The development of genomic resources for evolutionary significant species and natural

populations should be a priority, including non-model species that are close relatives of genetic model systems. The resources needed are not only whole-genome sequences, but also the genomics tools that make genetic manipulation possible. To make these resources available, however, evolutionary biologists will need to coalesce around a selected set of evolutionary model systems for genomic development.

- **Phenomic resources:** Evolutionary analyses of complex, integrated phenotypes are limited by the capacity to measure and analyze relevant phenotypes on large numbers of individuals in the context of evolutionary studies in the lab and field. Engineering resources for development of new technologies for automated, high-throughput phenotype measurement systems will be important to accomplish this task.
- **Large-scale experimental evolution:** Replicated, experimental studies of evolution at a regional to national scale would be invaluable for understanding short-term (1-100 year) evolutionary responses to environmental change in natural populations. The developing National Ecological Observatory Network (NEON) holds great potential for enabling such large-scale evolutionary experiments. Planning for instrumentation relevant to genetic and evolutionary analyses in the context of NEON is needed to achieve this potential.
- **Analytic resources:** Databases for phylogenetic, environmental, DNA sequence, and protein structure data are widely used and accessible, but comparable resources for phenotypic data are lacking. The conceptual tools needed to develop an appropriate standard for phenotypic metadata have not been developed. Just as importantly, the computational and analytical tools necessary to integrate data derived from phylogenetic, environmental, DNA sequence, protein, and phenotypic data have not been developed. Even tools for visualization and analysis of variation in complex phenotypes are largely lacking. Advances in all of these areas are needed to address many of the issues identified in this report.

## Appendix: Workshop participants

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