Studying the Evolution of Complex Adaptive Systems:

The Adaptive Dynamics Network Project

The central components of environmental systems are biotic, and these biotic components are often especially fragile. Populations of trees, crops, fish, mammals, and even viruses have a critical impact on the long-term stability of ecosystems and on the sustainable harvesting of renewable resources. Understanding the dynamics of such populations is therefore mandatory for any successful implementation of environmental management strategies, be they directed at the conservation of biodiversity or at the maximization of sustainable yields.

The biological record of different species offers an almost inexhaustible richness of generic as well as idiosyncratic properties, and a wide range of features are specific to particular systems. Yet unified approaches and powerful techniques are available from population ecology and evolutionary ecology, two overarching frameworks for describing, analyzing, and managing this huge variety. The field of population ecology primarily addresses changes in population abundance, while evolutionary ecology focuses on changes in the phenotypic compositions of biological populations (phenotypes are the targets of adaptation and can describe any structural or functional feature of an organism).

IIASA's Adaptive Dynamics Network (ADN) project operates at the forefront of research developments in both fields. ADN has been instrumental in creating the rapidly developing adaptive dynamics framework, which systematically links the fields of population ecology and evolutionary ecology and currently offers the most versatile tool for studying the evolutionary implications of ecological change. Particular applications include the sustainable management of renewable resources, the control of diseases and pests, biodiversity research, and conservation biology.

Since its inception, IIASA's ADN project has been successful in raising additional project funding. The European Science Foundation, through its Programme on Theoretical Biology of Adaptation, has supported three workshops, one on *Evolutionary Conservation Biology*, another on *Adaptive Speciation*, and a third on *Fisheries-Induced Adaptive Change* (to be held next year). The Austrian Ministry for Education, Science and Culture supported an ADN study on *Adapative Dynamics and Self-Organization*. The ADN project also is the recipient of a major European Union grant on *Modern Life-History Theory and Its Applications to the Management of Natural Resources* from the Human Potential Programme Research Training Networks. A major objective of the 3½-year project, scheduled to start in September 2000, is to train a number of young researchers in the methods and techniques for dealing with realistic environmental feedback in order to open new vistas for evolutionary ecology and resource management.

Evolutionary Time Scales: Shorter than Assumed

Evolutionary processes have long been thought of as being too slow to impinge on ecological management strategies. In contrast to this traditional view, recent empirical evidence shows that the effects of evolution may manifest themselves at time scales as short as two decades or less.

Several well-documented examples illustrate this assertion. One of the classic cases is the adaptation of the peppered moth. This moth has speckled gray wings and rests on tree trunks usually covered with gray lichens, against which the moth is difficult to see (Figure 1a). At the end of the 19th century, burgeoning industrial production in the United Kingdom and other parts of Europe resulted in atmospheric pollution that killed the gray lichen and darkened the trunks of trees. As a consequence, the previously well-adapted light-colored moths became very conspicuous (Figure 1b) and were thus exposed to heavy predation. This might well have doomed the moths to extinction. Within a few decades, however, the moths had adapted to their new environment by sporting a much darker wing

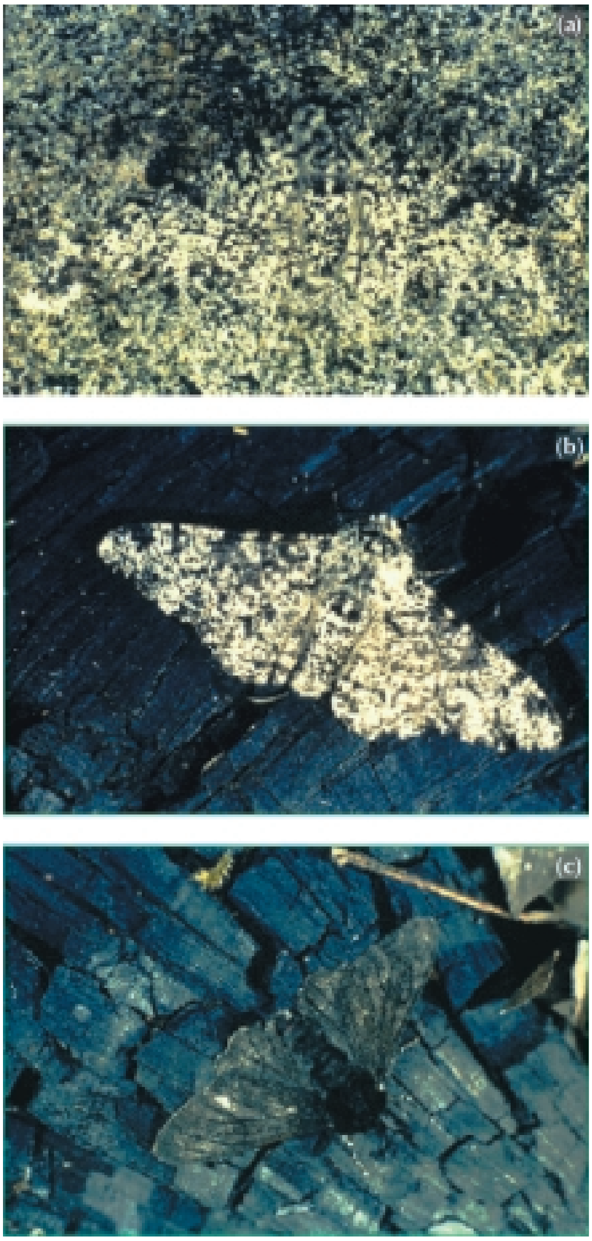

Figure 1: Industrial melanism. (a) Light-colored moth on a light background. (b) Light-colored moth on a dark background. (c) Dark-colored moth on a dark background. Photographs © Oxford Scientific Films.

coloration (Figure 1c). Interestingly, the decrease of air pollutants after the Second World War has led to rising frequencies of lighter forms of the moth.

Scientists are still vigorously debating the detailed evolutionary mechanisms that produced these changes, known as industrial melanism. Yet this example clearly demonstrates how quickly organisms can respond to environmental changes and how ecological predictions that do not account for such adaptations can be qualitatively in error.

Another instance of rapid evolutionary change was recorded in Australia. Rabbits introduced as a game species in the 19th century rapidly spread over the continent, causing great damage to agricultural crops and wreaking havoc on the vegetation basis for sheep farming. For this reason, a lethal virus was spread among wild Australian rabbits in 1950. The myxoma virus, imported from South America, initially killed about 99 percent of the rabbits infected. With this virus sweeping through the continent's wild rabbit populations, Australia had seemingly solved its rabbit problem for good. Within as few as five years, however, the virus had evolved toward lower levels of virulence (measured in terms of rabbit mortality, see Figure 2a), and by 1958 the rabbits had adapted to the presence of the new virus by becoming much more resistant (Figure 2b). Because of these rapid adaptations, the original projections of rabbit populations quickly became obsolete. In 1996, Australian government scientists initiated another lethal epidemic by releasing the rabbit calcivirus. A further bout of coevolution can be expected.

Other examples of rapid evolutionary change include the emerging antibiotic resistance of many diseases (see article, page 9), rapid adaptations to changes in habitat temperatures and predation pressures, evolved resistance of plant populations to heavy-metal toxins, and life-history changes in commercially exploited fish stocks (see article, page 6). All these findings point to the same conclusion: if we are to manage ecosystems in a sustainable manner, we must take rapid adaptations into account.

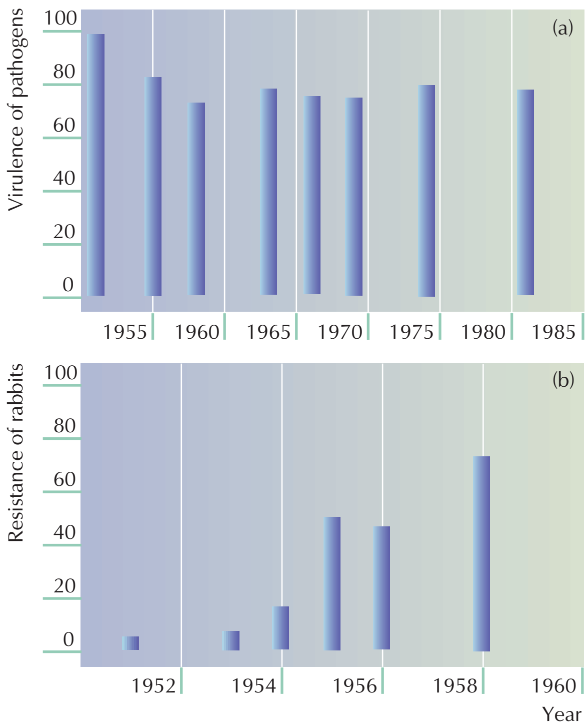

Figure 2: Host–pathogen coevolution. (a) The virulence of the myxoma virus quickly decreased after its introduction into the wild rabbit populations of Australia. (b) At the same time, the resistance of rabbits rose quickly.

Adaptive Dynamics Theory

Whenever an ecological system adapts, it affects its environment (Figure 3). Yet, evolutionary research has traditionally ignored this feedback loop. Consider the myxoma virus and its host, the European rabbit in Australia. Once the virus had evolved a lower virulence, the density of rabbits increased. This change in the virus's environment in turn affected the way the virus spread. Likewise, by the time rabbits had evolved higher resistance, the proportion of rabbits carrying the virus had changed. This change influenced the likelihood that a rabbit would become infected, and thus the demography of the rabbit population. Such so-called environmental feedbacks are critical for describing adaptive change in natural systems. The key advance achieved by adaptive dynamics theory is closing the environmental feedback loop in a general manner.

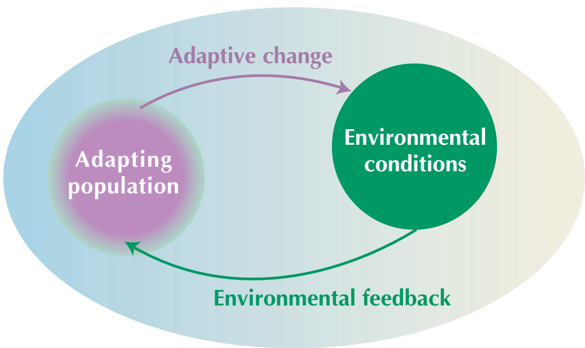

Figure 3: Environmental feedback. Adaptive change depends on environmental conditions, which in turn are altered by adaptive change.

The fitness of organisms can only be evaluated relative to the environment in which they live. Because of the feedback just described, this environment depends on the current adaptive state of the population under consideration. To assess the fitness of a mutant variant, researchers must therefore specify the resident form against which the variant is competing. If the mutant has an advantage compared with the resident—in other words, if it has positive fitness—it will spread through the population and eventually replace the resident. By contrast, if the mutant has negative fitness, it will quickly become extinct. Mutants that have the same adaptive trait as residents are always neutral, that is, they have zero fitness.

So-called pairwise invasibility plots (Figure 4) allow researchers to analyze which mutants can invade which resident populations. In a way popularized by the ADN project, the sign structure of these plots determines the expected course of evolutionary change.

One of the surprising findings of adaptive dynamics theory is that continual invasion of advantageous mutants can cause a unimodal trait distribution to

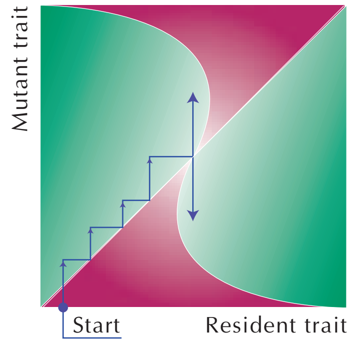

Figure 4: Pairwise invasibility plot. Green regions indicate mutants with an evolutionary advantage (positive fitness), red regions correspond to mutants that are deleterious (negative fitness) relative to the resident. Note that the range of advantageous mutants changes with the state of the resident population, reflecting the effect of environmental feedback. The arrows indicate a possible sequence by which evolutionarily advantaged mutants replace residents.

become bimodal (Figure 5). The phenomenon, known as evolutionary branching, can occur in all ecological systems that exhibit sufficiently strong environmental feedback. The cause for branching is easy to grasp: an adaptation that would be optimal if individuals were alone can become unattractive once all individuals of a population are using the same adaptive strategy. The process is akin to the boom and bust of gold rushes—with few diggers, revenues were high, until too many competitors eventually made the digging uneconomical. Studies of evolutionary branching have opened up new avenues for understanding the origin of new species, the composition of ecological communities, and the formation of biodiversity (see also page 19).

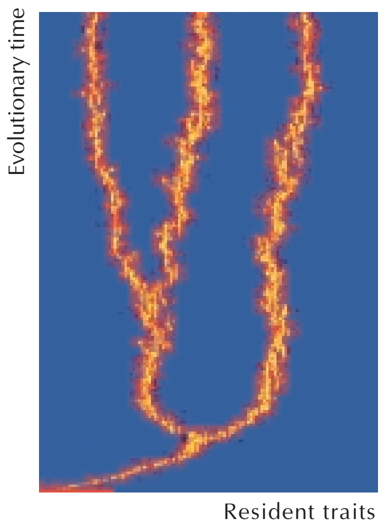

Figure 5: Evolutionary branching. Under the influence of environmental feedback, a unimodal distribution of residents can become bimodal.

The expected rate of long-term evolutionary change can be described by the following canonical equation of adaptive dynamics:

$$\frac{d}{dt}s = \frac{1}{2}\mu\sigma^2 n(s)\frac{d}{ds'}f(s',s)\Big|_{s'=s}$$

where s is the adapting trait, ds/dt is its evolutionary rate, μ is the probability that a mutation will arise during reproduction, σ is the average mutational step size, $n(s)$ is the population size when trait s is resident, and $f(s',s)$ is the fitness of a mutant s' in a resident population s. The partial derivative $df(s',s)/ds'|_{s'=s}$ ensures that traits evolve in the direction of advantageous mutations. This direction, however, can change as a result of environmental feedback.

Advances in Modeling Techniques

Studies of ecological dynamics and biological adaptations have often suffered from excessive hype attached to particular brands of models. This applies to the ecosystem models created by the International Biological Program of the early 1970s and to the recent rise of individual-based models in ecology, as well as to some (otherwise fascinating) research on Artificial Life.

IIASA's Adaptive Dynamics Network attempts to steer around this potential pitfall by following a four-tiered strategy. First, ADN employs a careful blend of analytical and numerical approaches in its research. The mixture of these techniques is mutually illuminating and often offers a viable compromise between the Scylla of oversimplification and the Charybdis of intractability. Second, instead of applying only available, mainstream methods, ADN constantly expands the scope of its techniques in directions that make it possible to deal with increasingly complex ecological scenarios. This problem-driven agenda has already led to a variety of methodological innovations that scientists worldwide have begun to recognize and apply to their own work. Capitalizing on IIASA's tradition of interdisciplinary research, ADN strives to bring together biologists, mathematicians, physicists, and computer scientists to develop and translate promising approaches into new areas of investigation.

Third, many studies in the ADN project explicitly bridge the gap between abstract analysis and practical applications. Often the most successful way to promote a methodological advance is to demonstrate precisely how it can contribute to addressing relevant questions that were previously deemed infeasible. For example, ADN's research on how fishing affects the Northeast Arctic cod (see article, page 6) responds to a need already highlighted by marine biologists. Fourth, ADN recognizes that most ecosystems are so complex that a long time will pass before scientists can begin to understand or analyze them in a comprehensive manner. Instead of embarking on a "Mission Impossible," ADN has found it essential to focus on those research tasks that are just becoming tractable while offering new insights into the inner workings of ecological and environmental dynamics. Such targeted studies usually have a local or regional geographic scope, but are selected for their global and universal relevance.

A Pivotal Role

In summary, IIASA's Adaptive Dynamics Network fosters the development of new techniques for understanding the evolution of complex adaptive systems. This research promotes and is guided by several carefully chosen case studies that focus on critical aspects of ecosystem analysis and management.

ADN pursues its mission within an extended network of international collaborators, involving more than 35 partner groups in 15 countries (Figure 6). This

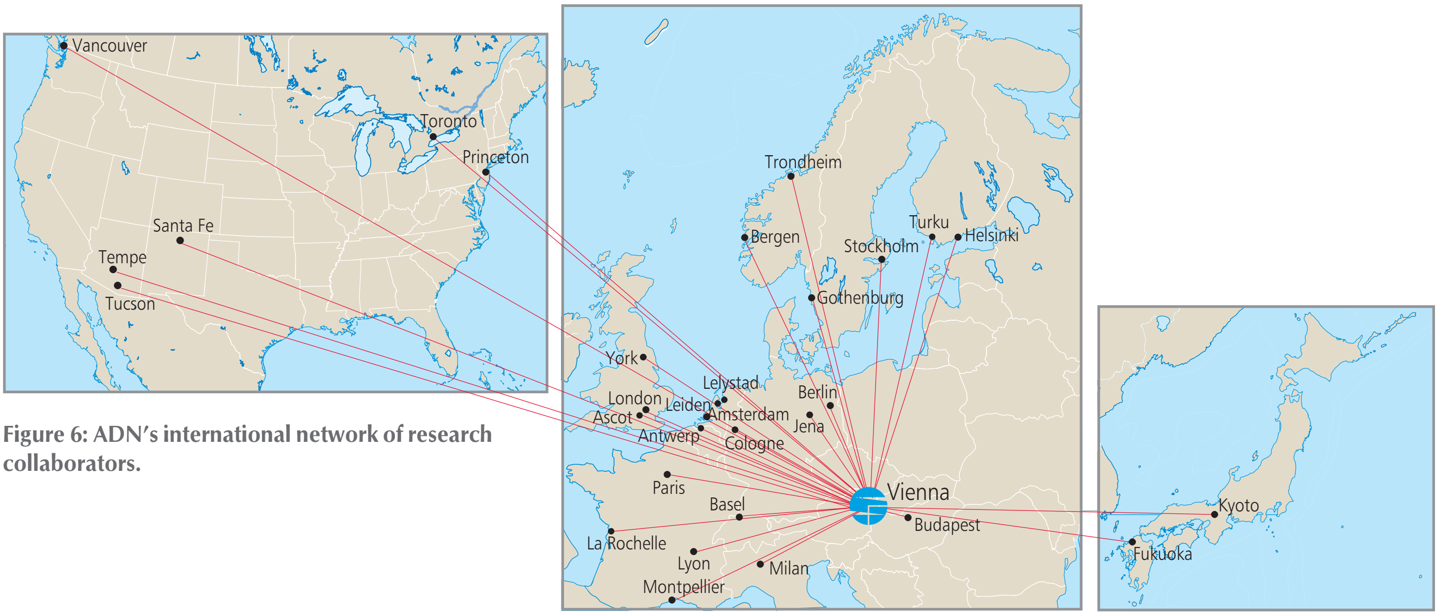

Figure 6: ADN's international network of research collaborators.

decided orientation toward collaborative research ensures the widest possible dissemination of results obtained at IIASA and thus makes the best use of the resources IIASA offers. Moreover, serving as a central node within the adaptive dynamics research community is a critical element of ADN's agenda. This role gives ADN the credibility needed to offer guidance into uncharted scientific territory. Annual workshops on a variety of topical subjects (including spatial ecology, the evolution of infectious diseases, evolutionary conservation biology, speciation research, and fisheries management) strengthen ADN's scientific basis, broaden its scope, and ensure wide visibility and critical discussion of novel findings. In the same vein, ADN staff serve as series editors for a newly established line of books published by Cambridge University Press: the *Cambridge Studies in Adaptive Dynamics*.

Over the past few years, ADN's innovative methodology has spread rapidly within the international research community. On this basis, the project leads the efforts that bring the resulting new insights to bear on pressing ecological and environmental problems.

For more information, see IIASA's ADN Web page www.iiasa.ac.at/Research/ADN.