IIASA
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spring '00

Moving targets: Understanding adaptation in natural systems

Biodiversity

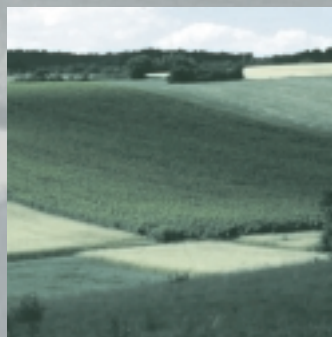
Virulence evolution

Ecology

Adaptation

Genetic changes

Landscape succession



options

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Options is a magazine featuring the activities of the International Institute for Applied Systems Analysis (IIASA), located in Laxenburg, Austria. IIASA is an interdisciplinary, nongovernmental research institution sponsored by a consortium of National Member Organizations in Asia, Europe, and North America. The Institute's research focuses on sustainability and the human dimensions of global change. IIASA's studies are international and interdisciplinary, providing timely and relevant insights for the scientific community, policymakers, and the public.

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This issue of *Options* highlights the activities of IIASA's Adaptive Dynamics Network (ADN) project. The ADN project brings together the fields of population and evolutionary ecology with a long-term goal of developing ways of improving sustainable management of renewable resources. In its work, ADN continues the tradition of excellence in ecological research at IIASA—a tradition reaching back to the late 1970s and early 1980s, when Crawford S. (Buzz) Holling, leader of IIASA's Ecology and Environment Project from 1973–1975 and Director of IIASA from 1981–1983, led the classic spruce budworm study linking nonlinear population dynamics with real-world forest management. In 1994, one of Holling's early collaborators, Karl Sigmund, suggested that IIASA should strive to regain international prominence in ecological research by establishing a new activity.

In autumn 1994, following a review of the Institute's ongoing work by a panel of 14 distinguished ecological scientists, IIASA established an activity that initially was centered on two subjects: dynamics of biological invasion and viability analysis of ecological communities. In 1998, we converted the activity, then a part of the Dynamic Systems project, into a full-fledged project, with Hans Metz as the leader and Ulf Dieckmann as the in-house coordinator. Metz and Régis Ferrière, two biologists, Dieckmann, a physicist, and Sigmund, a mathematician, form the core leadership of the ADN project, which is revolutionizing thinking about how ecology can be applied to the management of renewable resources.

The current issue of *Options* illustrates the rich variety of topics the project has examined with significant and startling results. ADN's work has been published in a number of prestigious journals and forms the basis of a multi-volume book series, the *Cambridge Studies in Adaptive Dynamics*, published by Cambridge University Press. One of the many findings of ADN's research is that evolutionary changes in many species take place much more rapidly than scientists previously considered possible. Evolution in populations of microscopic viruses and bacteria is already known to proceed at short time scales. Various studies have now demonstrated that also higher organisms can rapidly adapt within a few decades or even years. These findings have profound implications for management of macroscopic renewable resources: to be effective, such efforts must take into consideration possible evolutionary processes that contribute to determining a population's characteristics at time scales of concern to ecological management.

For an in-depth look at the ADN activities outlined in this issue, readers can turn to the IIASA Web site. The IIASA Web site is being redesigned to ease access for outside users. We anticipate that in the years to come, the number of visitors to the IIASA Web site, which were in excess of a million in 1999, will continue to grow. The IIASA Web site will play an increasing role in informing scientists, policymakers, and the public of the exciting, innovative science carried out at IIASA, of which ADN is a prime example. I invite all those interested in learning about IIASA and its policy-oriented research program to visit the IIASA Web site on a regular basis: www.iiasa.ac.at.

Gordon J. MacDonald, Director

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

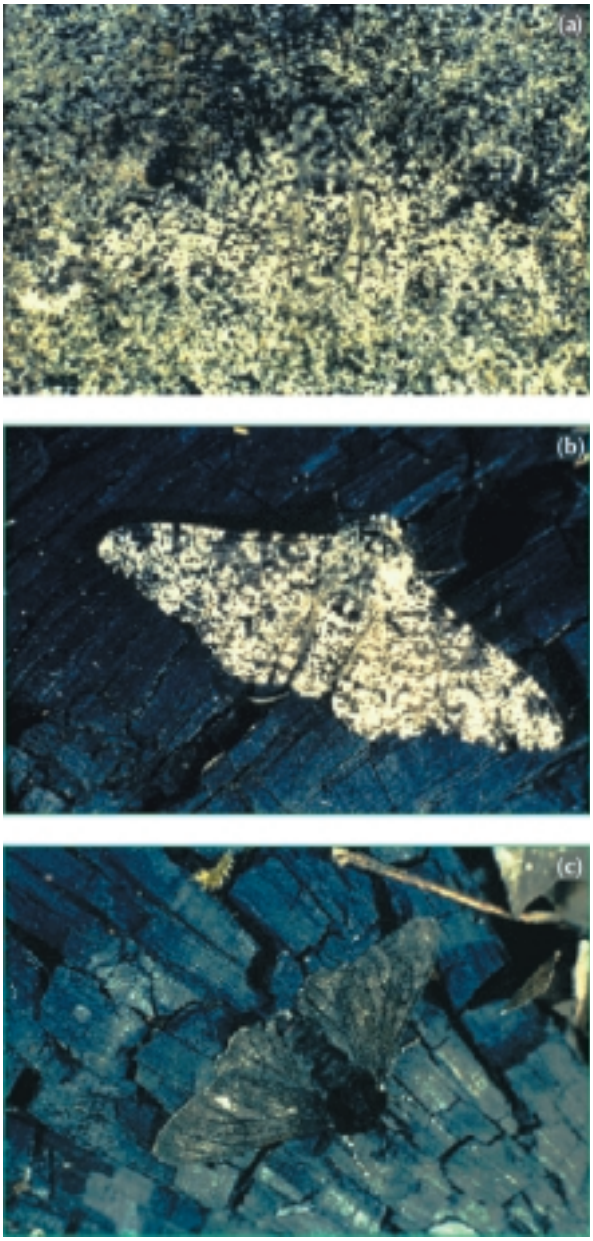


Figure 1: Industrial melanism. (a) Light-colored moth on a light background. (b) Light-colored moth on a dark background. (c) Dark-colored moth on a dark background. Photographs © Oxford Scientific Films.

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.

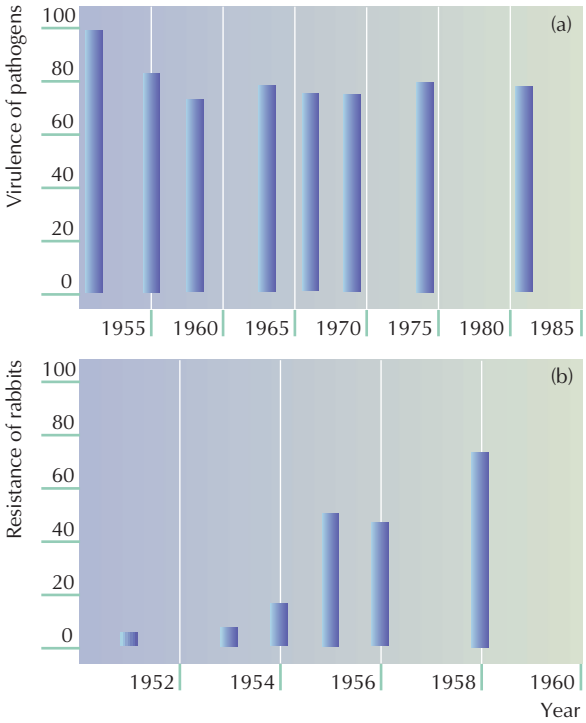


Figure 2: Host–pathogen coevolution. (a) The virulence of the myxoma virus quickly decreased after its introduction into the wild rabbit populations of Australia. (b) At the same time, the resistance of rabbits rose quickly.

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.

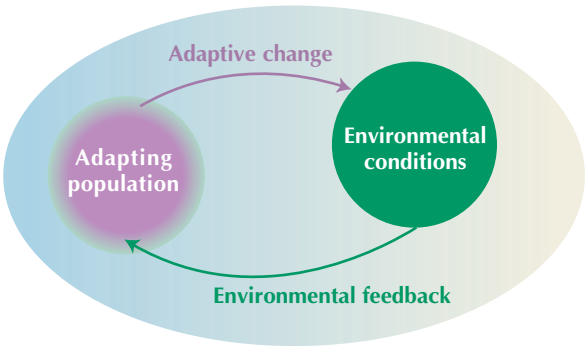


Figure 3: Environmental feedback. Adaptive change depends on environmental conditions, which in turn are altered by adaptive change.

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 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).

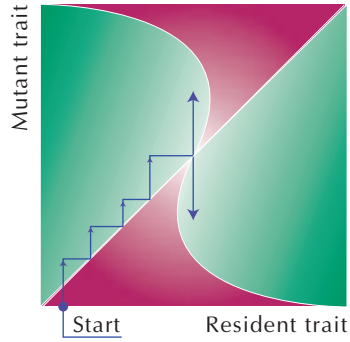


Figure 4: Pairwise invasibility plot. Green regions indicate mutants with an evolutionary advantage (positive fitness), red regions correspond to mutants that are deleterious (negative fitness) relative to the resident. Note that the range of advantageous mutants changes with the state of the resident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

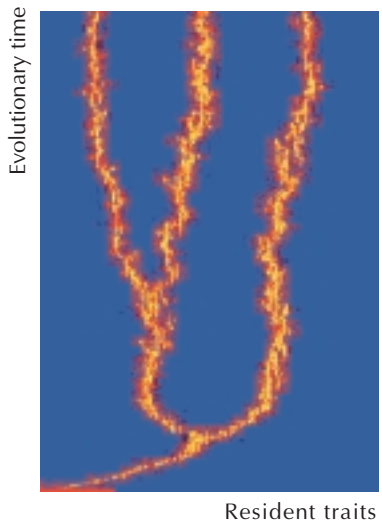


Figure 5: Evolutionary branching. Under the influence of environmental feedback, a unimodal distribution of residents can become bimodal.

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

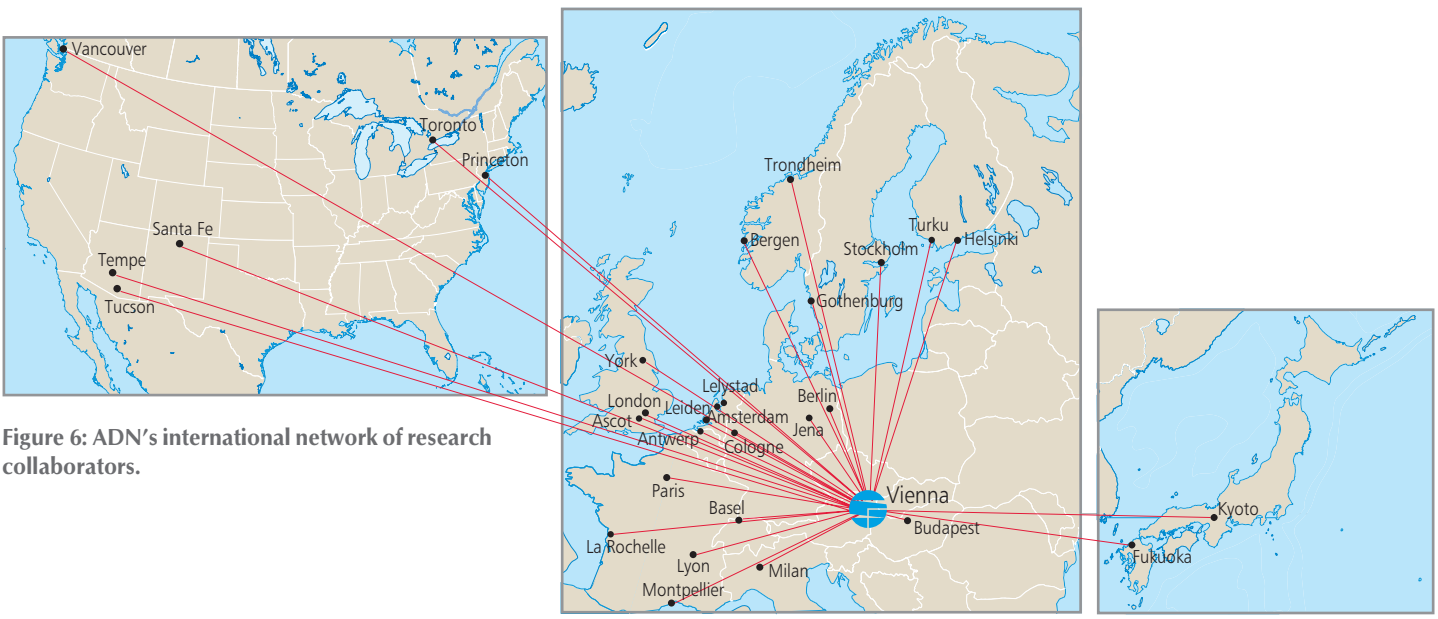


Figure 6: ADN's international network of research collaborators.

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.

Shrinking Cod: Fishery-Induced Change in an Oceanic Stock

Fishing is a major source of food and other resources for humankind. Today most marine fish stocks are heavily exploited, and many are overexploited. Such intensive utilization has raised concerns about the sustainability of the modern fishing industry. Can the current level of catches be maintained in the long run, or are we running the risk that some stocks will collapse and the corresponding commercial fisheries will have to be closed?

In addition to having obvious effects on harvested species, fishing influences other, nontarget species. Those that utilize the target species as their own prey suffer, whereas those preyed upon by the target species or those that can feed on discarded fish benefit (Figure 1). These effects may cascade to other species in a food chain and can cause undesired impacts on biodiversity and ecosystem functioning.

Figure 1: The kittiwake is one of the winners in the expansion of trawling fisheries. Kittiwakes regularly follow fishing vessels far offshore, feeding on discarded fish.

Fisheries scientists and managers have increasingly begun to appreciate the diverse ecological implications of marine exploitation. However, they have not yet widely acknowledged that fishing can exert strong selective pressures on exploited stocks and may thus change their genetic composition. One particular type of selection arises as a direct consequence of elevated mortality. When fishing pressure increases, it becomes increasingly likely that a fish that matures late will be caught before it has a chance to spawn. Such a fish leaves no descendants. Intensive fishing is therefore expected to select for an earlier age at first spawning. Such a change has a problematic consequence for the fishing industry: because a fish's growth slows after maturation, the average size of the fish decreases and with it the commercial value. These effects should be strongest, and especially evident, in fish with traditionally late maturation, such as cod, halibut, and many other large, bottom-dwelling fish species.

In collaboration with the Institute of Marine Research in Bergen, Norway, IIASA's Adaptive Dynamics Network (ADN) project has screened the largest cod stock of the Northeast Atlantic, the Northeast Arctic cod (*Gadus morhua*), for the occurrence of fishery-induced adaptive changes. In terms of productivity, these fish constitute one of the most important stocks in northern Europe. The Northeast Arctic cod is particularly well suited for such an analysis. The primary reason is the availability of detailed long-term data sets that document the cod's properties over the course of the 20th century. Moreover, this stock has experienced a well-documented change in harvesting pattern that is expected to make any adaptations induced by fishing practices particularly obvious.

The Northeast Arctic cod feeds in the Barents Sea. From there, mature fish undertake an annual migration to the spawning grounds near the Lofoten Islands off the Norwegian coast (Figure 2). The cod congregate in the spawning grounds in early spring, presenting an easy target for fishermen; estimates place mortality at between 20 and 30 percent of the spawning fish. The

Figure 2: Spawning and feeding ranges of the Northeast Arctic cod.

highly productive spawner fishery at the Lofoten Islands has a very long history of exploitation: the first record of this fishery is found in *Egil's Saga*, which dates back to the 9th century.

Historically, the Northeast Arctic cod has matured late, with a mean age at first spawning of about 10 years. Scientists believe that the centuries of fairly intensive exploitation at the spawning grounds have been partially responsible for this late maturation. When faced with a high risk of being caught at the spawning grounds and low levels of mortality at the feeding grounds, fish that delayed their maturation had an advantage. This allowed them to stay at the feeding grounds until a later age, and thus to grow to a larger size before arriving at the spawning grounds, where the risk of being caught was high. Because a cod's fecundity strongly depends on its size, delayed maturation paid off in terms of increased numbers of offspring expected (Figure 3).

Figure 3: Large female cod from the beginning of the 20th century, weighing 30 kilograms. Cod of this size are no longer found. Photograph by Anders Beer Wilse, courtesy of the Norsk Folkemuseum, Oslo, Norway.

However, the pattern of exploitation has changed drastically since the early 20th century. The development of modern motor-powered trawler fishing in the late 1920s enabled offshore fishing at the feeding grounds in the Barents Sea. In fact, since the Second World War, most fishing effort has concentrated on the Barents Sea, with annual mortality often exceeding 40 percent of the fish population. A key factor here is that, as opposed to the spawner fishery, the feeder fishery is unselective with regard to maturation status. The current fishing mortality is actually so high that only a small fraction of fish survive to maturity; consequently, the current catch consists mostly of tiny, immature fish (Figure 4). Under the new exploitation regime, earlier maturation has therefore become advantageous.

Figure 4: Catch from a survey haul, consisting mostly of cod.

Thus, the Northeast Arctic cod has undergone a change from a harvesting pattern that should favor late maturation to a pattern favoring early maturation. This hypothesis is in agreement with observations that show a clear trend toward earlier maturation of the Northeast Arctic cod, with a decrease of about three years in the mean age at first spawning from the 1940s until today (Figure 5). Because age at first spawning is a heritable characteristic, the data seem to support the hypothesis that the Northeast Arctic cod has responded evolutionarily to the altered exploitation regime.

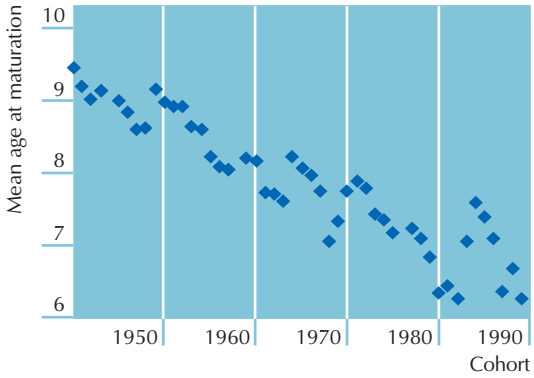


Figure 5: Decrease in the mean age at first spawning in the Northeast Arctic cod.

An alternative hypothesis, however, attributes this shift to environmental changes and does not imply an altered genetic composition of the stock. The reasoning is that as a result of intensive exploitation, the stock biomass has declined from an estimated 4.2 million tons right after the Second World War to below 1 million tons in the 1990s. This decline in biomass has resulted in better feeding conditions for those fish that remain; consequently, the growth rate of juvenile cod has increased. It is a common observation that fish mature at earlier ages if growth conditions improve; therefore, increased growth rates resulting from fishing

could also explain the observed decline in the age at first spawning.

Is it possible to distinguish between the two hypotheses for explaining the observed changes in age at first spawning? The answer is yes. IIASA's ADN project has disentangled the effects of changed growth conditions from those of genetic change by investigating changes in a compound trait known as the reaction norm of maturity, which relates age to size at first spawning. Analysis of this trait has allowed ADN to remove from the data most of the effects of varying growth rates (Figure 6). The residual variation in the maturation data investigated is then likely to have resulted from genetic effects.

After developing the necessary statistical methodology, ADN researchers studied the reaction norms for a data set of the Northeast Arctic cod collected by the Institute of Marine Research in Bergen. The data include information about cohorts from 1923 onward, thus covering the period during which the responses to the exploitation pattern should become manifest. The results show a

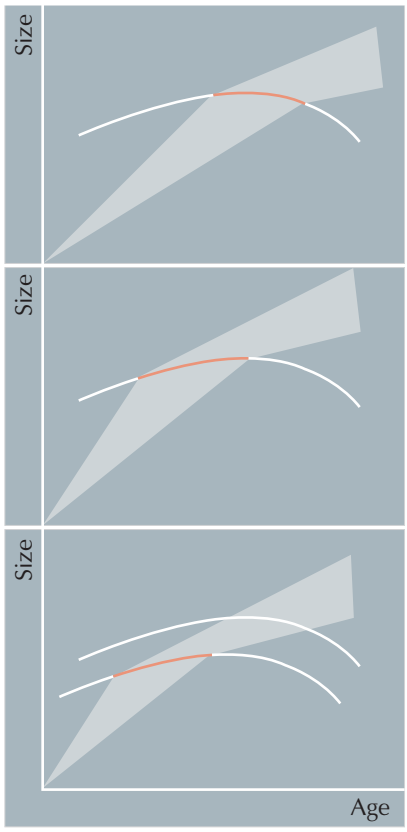


Figure 6: Reaction-norm analysis reveals whether change in maturation results only from improved growth conditions (change from *top* to *middle*) or must be attributed to genetic change (from *top* to *bottom*). In these graphs, individuals are considered mature at the point where their growth trajectory passes through the reaction norm curve; the shaded regions give the range of growth trajectories in the population.

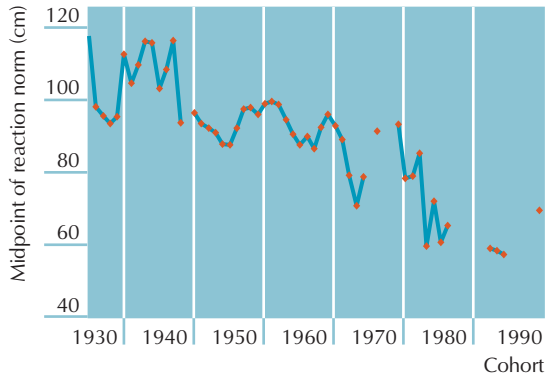


Figure 7: Change in the midpoint of the reaction norm at age eight for the cohorts 1925–1990. The midpoint gives the length of fish at which probability of maturation is 50 percent.

continual decline in the reaction norm for age and size at maturity (Figure 7). In other words, present-day cod mature at a much younger age and smaller size than their ancestors at the beginning of the 20th century would have done when faced with similar growing conditions. This conclusion supports the hypothesis that exploitation pressures have caused changes in the genetic composition of the Northeast Arctic cod; thus the observed life-history changes cannot be fully explained only by the ability of fish to show plastic responses to improved feeding conditions.

Why should we care about genetic changes in fish stocks? First, and most important, changes in traits such as age at first spawning influence the productivity of the stock. When maturation takes place earlier, we can expect the sustainable yield from a stock to decline. Second, the average size of fish is expected to decrease, further diminishing the market value of catches. Third, if the observed changes in maturation have a genetic component—as now seems to be the case—the deterioration in yield will not easily be reversed, even if the fishing industry takes steps to alter harvesting patterns. Genetic recovery occurs much more slowly than ecological recovery. It is therefore in the interest of fisheries managers to prevent unwanted genetic changes as early as possible.

It is not yet known how many fish stocks have been strongly affected by fishing practices or how many are currently under threat of genetic change. At any rate, however, the precautionary principle in fisheries, as highlighted in United Nations declarations and in agreements about biodiversity, mandates increased awareness of this issue. ADN's fisheries research provides crucial evidence for policymakers concerned with ecology and with the world's food supply.

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

From Black Death to Red Queen

Biologists and mathematicians have become increasingly interested in the evolution of virulence—the mortality due to an infection—and the corresponding "Darwinian medicine," which seeks an evolutionary explanation for vulnerability to disease. The interaction of these elements constitutes one of the most fascinating chapters in the theory of evolution. It offers a major application for adaptive dynamics, a branch of biomathematics in which IIASA's Adaptive Dynamics Network (ADN) project plays a leading role. The huge size of the populations of pathogens, their rapid turnover rate, and their variability provide an ideal basis for capturing rapid adaptation in mathematical models. Obvious clinical and social incentives ensure that these models will be modified and improved by experimental tests.

The scene could have come straight out of a science fiction film. A team of scientists crowded into a desolate graveyard on a windswept arctic island and proceeded to excavate, with specially devised high-tech tools, the frozen corpses of miners buried 80 years ago. The security measures were tremendous, and not without reason. The miners had died from Spanish influenza, and their frozen corpses were likely to contain traces of the virus responsible for the deaths of more than 20 million people worldwide.

What looked like the newest Spielberg movie was part of an abortive attempt to analyze the genome of the virus and understand the reasons for its lethal effects. Flu viruses, after all, are usually relatively harmless. What mutation had caused the rabid virulence that led first to the disease's blitzkrieg-like global expansion and then to its speedy extinction? Indeed, once the Spanish flu had caused either death or an immune reaction in more than a quarter of the human population, it had depleted its reservoir of potential hosts. From the pathogen's viewpoint, inordinate aggressiveness is ultimately self-defeating.

The Private Biosphere

Spectacular advances in micro- and molecular biology were necessary before scientists could appreciate the diversity of the ecosystem beneath our skin and the ferocious battles that the immune system fights on an almost daily basis against pathogen invaders. Each infectious disease represents a world war in the individual's private biosphere.

Human immunodeficiency virus (HIV) patients offer possibly the most telling example. As is well known, full-blown acquired immunodeficiency syndrome (AIDS) develops only some 10 years after infection. It used to be thought that this corresponded to a "latency" in the course of the disease: that the insidious virus feigned death to allow its host to infect as many new contacts as possible. On the contrary, a fierce guerilla battle rages in the host's body throughout this period. Billions of free virus particles are produced daily and usually eliminated within a few hours by a still overwhelmingly strong immune system, unless they manage to find refuge in some pocket of resistance, such as the lymph nodes.

HIV is particularly prone to mutation, so new variants constantly emerge within each host during the hectic replication of the virus. These ceaseless threats present constant challenges to the immune system's ability to adapt. It can meet every new variant, but not all at the same time. After some 1,500 generations of HIV, the diversity overwhelms the immune response, which collapses like a militarily strong empire attacked on too many fronts.

The mathematical models of Martin Nowak provide a detailed picture of the actual course of the disease. Immediately after infection, the HIV population, still homogeneous, grows quickly. This alerts the immune system, which "learns," through a complex mechanism that selects among tens of thousands of different antibodies, how to recognize the virus and combat it. But HIV keeps producing ever-new variants able to escape the highly specialized killer cells present and to grow until the immune system devises a new response. About one-third of infected cells are destroyed daily. This ferocious little war lasts for years. The number of HIV particles remains relatively low compared with the initial phase (i.e., before the immune system is fully alarmed), but its genetic diversity grows inexorably. In the end, the immune system becomes unable to respond on all fronts. During the final phase, characterized by the emergence of fully developed AIDS,

the number of HIV particles shoots up and infests the patient's bloodstream.

According to this view, still hotly debated and currently undergoing clinical tests, AIDS develops whenever the diversity of the virus exceeds a certain threshold. This theory typifies a new view of infectious diseases, which draws its inspiration from population ecology. Knowledge of the molecular interactions between pathogens and antibodies now supplements improved understanding of the dynamics of the feedback loops that regulate the interacting populations of pathogens and antibodies, feedbacks as complex as those in more familiar ecosystems.

Often, only mathematical models allow us to analyze these feedbacks accurately. As an example, HIV-infected cells stimulate the immune system to produce so-called cytotoxic lymph (CTL) cells. This leads to oscillations: the more infected cells, the more CTL cells, which makes for fewer infected cells, and hence fewer CTL cells, etc. This pattern closely resembles the population dynamics of predators and prey, and can lead to oscillations that are damped (regular) or periodic. If mutant viruses appear that can escape the search image of the CTL cell, the scenario leads to highly complex cycles. The mutant virus suddenly upsets the seemingly static equilibrium of viruses and their CTL foes. The population of the appropriate new CTL cell starts to grow, but after a period of standstill the resulting equilibrium will be replaced by a return of the previous type of virus, and its specialized CTL cell, and so on. This game of cat and mouse repeats constantly, but not periodically: the sudden upheavals occur ever more rarely, seemingly without warning. Even clinically clean mathematical equations allow no precise long-term predictions.

The Parasite as Milker or as Butcher

HIV is particularly variable, but other parasites are also prone to frequent mutations. The variants undergo ceaseless selection: whichever multiplies fastest has an advantage. But the race within the host organism is only the first stage in the parasite's spread. What is important is infecting others: making the transition from one host to another. The parasite uses the host organism not only as a resource, but also as a vehicle—a second-order body. The interplay between the selective pressures within and between hosts regulates the pathogen's virulence.

The virulence of infectious diseases changes rapidly. The classic example is the myxoma virus, which was intentionally imported to Australia in 1950 to fight the uncontrolled spread of rabbits (which had also been imported). As it turned out, scientists had misjudged the effectiveness of this measure. Whereas only 1 out of 500 infected rabbits survived in the first year, soon three out of four managed to recover. Many human infections exhibit a similar trend toward harmlessness. For instance, when syphilis first appeared in Europe, it was incomparably more virulent than in later centuries: the flesh literally fell off the victim's body. Scarlet fever is much less dangerous today than it was even 50 years ago.

For a while, this tendency was deemed a universal law, easily explained by conventional wisdom: obviously, parasites prosper if they can take longer-lasting advantage of their host. Such epidemics as the Spanish flu or the Black Death—the bubonic plague that killed more than a quarter of Europe's population in the 14th century—destroy their own resources and eventually are unable to find new victims, thereby effectively destroying themselves. It does not pay for the parasite to kill its host rather than milk it.

Unfortunately, this view turned out to be overly optimistic. Mathematical models by R. M. May and Roy Anderson showed that natural selection among microparasites tends to maximize the average number of infections caused by one infected host in an otherwise uninfected population. Thus, an increase in virulence does not always reduce transmissibility; this depends on the details of the infection. For instance, if a cold causes heavy sneezing, it has better chances of spreading, but if it causes its victim to stay in bed, it will lose infectiousness. By contrast, pathogens transported by mosquitoes (such as malaria or yellow fever) suffer no disadvantage if the host cannot move. The American virologist Paul Ewald has shown that the same holds for typhoid fever and cholera, diseases that spread via contaminated drinking water. In those regions of India where the water supply was purified, endemic cholera became not only rarer, but also milder. On the other hand, not all progress in sanitation leads to a decline in virulence.

Doctors and orderlies may actually improve the transmissibility of a disease by treating patients in hospitals.

As soon as several strains of parasites have infected a host, the virulence of each increases. This phenomenon is similar to the "Tragedy of the Commons": restraint can only benefit rivals. This competition among exploiters can lead to the extinction of their host, and subsequently of its parasites.

Arms Races

Obviously, natural selection impels not only the pathogens but also the immune systems of their hosts toward better and better adaptations—within individual hosts and host populations. The situation resembles an arms race between determined foes. Every new infection in the host organism causes a frantic search for the most appropriate antibody among tens of thousands, followed by its mass production. This response explains not only why the organism will subsequently be immune to other, possibly even more virulent, infections of a similar type, but also why vaccines are effective. Usually this type of immunity cannot be inherited, but those genetic immunotypes that react best against the prevailing infections will spread from one generation to the next.

This evolution of the host organisms provides another reason for the declining virulence of those pathogens that have plagued a population for a long time. History, particularly from the time of the great geographic discoveries, abounds in examples of diseases that devastated populations encountering them for the first time. Measles, smallpox, and typhoid fever eradicated entire tribes from the American continent. Why did Europeans exhibit such superior immune responses? Simply because many of their preceding generations had already confronted these diseases. The Native Americans, of course, had their own diseases, so why did these remain relatively harmless to the Europeans?

UCLA professor of physiology and author Jared Diamond has proposed an astonishing answer in his book *Guns, Germs and Steel*. During their conquests, Europeans showed greater resistance to new diseases because they had domesticated many more species of animals than had the Native Americans. Human diseases often originate when parasites from another species discover humans as new hosts. HIV, for instance, descends from the simian immunodeficiency virus, a harmless virus widespread among apes. We have inherited most types of flu virus from birds, and domestic animals have provided an inexhaustible well of plagues. Thus, more important than the horses of the conquistadors were the pigs and poultry in whose droppings their forebears had wallowed.

That the evolution of immune responses can keep abreast of that of pathogens seems like a miracle: parasites have a much shorter generation span and higher mutation rates than their hosts. Bacteria that have acquired resistance to antibiotics provide a sad example of this rapid evolution. For 50 years, another arms race has pitched pharmaceutical companies against infectious bacteria, and the bacteria appear to be winning. It has become increasingly difficult to develop new antibiotics. Some pharmaceutical enterprises have already given up.

The Scent of Love

Sexual replication offers the most important defense of hosts against the speedy adaptation of parasites, because it mingles the parental immunotypes in ever-new recombinations. An immune system resembles a numeric code; parasites resemble hackers that constantly attempt new combinations of digits to crack that code. The host organism cannot afford to remain stuck with the same code for too long. An effective immune system must be rare, because as soon as it becomes frequent, it will succumb to the multiple decryption attempts. Thus, immune systems must change continually to avoid becoming sitting ducks for parasites.

Many biologists currently favor the Red Queen hypothesis as an explanation for the prevalence of sexual replication. The theory draws its name from a character in Lewis Carroll's *Through the Looking Glass*; in her country, says the Red Queen, "it takes all the running you can do, to keep in the same place." Again, this field is dominated by mathematical models, which show that asexual populations suffer from evolutionary disadvantages. Sexual replication causes undamped, irregular oscillations in the dynamics of coevolution that prevent the extinction of rare genotypes and guarantee a steady supply of alternative options.

Thus, choosing a mate whose immunotype is as

different as possible from one's own is usually most profitable in terms of ensuring healthy future offspring. Experiments have shown that sexually reproducing populations actually adapt this strategy when they select mates. For example, female mice favor males with a different major histocompatibility (MH) complex, an important part of the immune system. They use their sense of smell to identify these males—doubtless a remarkable ability!

Even more remarkable, humans share this ability without being aware of it. In an extremely simple experiment, Claus Wedekind has shown that humans can distinguish the smell of complementary MH complexes. Young women were asked to rate the smell of T-shirts that had been worn by male test subjects for several nights. The women showed a significant preference for the scent of men who had complementary MH complexes. In addition, the favored smell often reminded the test person of the smell of an actual partner—a clear hint that the olfactory preference had an effect not only in the laboratory, but also in the choice of a partner for the disco and the bed.

From major turning points in world history, such as the conquest of America, down to our most intimate preferences, the evolving virulence of our germs has profound implications for our lives and offers new challenges to the mathematical analysis and numerical simulation of amazingly complex adaptive feedback loops. Some of the major motivations and applications of ADN's work stem from problems related to the evolution of virulence. IIASA's research efforts may pave the way toward an ambitious goal—the management of virulence in populations throughout the world.

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

Adaptive Responses to Environmental Threats: Evolutionary Suicide, Insurance, and Rescue

Many plant and animal species around the world face the danger of extinction, largely as a result of human activities. To be effective, conservation and restoration must be carried out in the context of comprehensive landscape and ecosystem approaches that consider biodiversity and large-scale ecological processes. At the same time, smaller-scale species- and population-based approaches must also play an essential role in developing and monitoring regional strategies to ensure proper management of ecologically important species, or those that indicate ecosystem health.

All factors affecting species extinction risk ultimately manifest themselves, and can be evaluated, in terms of population dynamics. The emerging field of evolutionary conservation biology seeks to determine if populations or species can respond to changing selection pressures rapidly enough to forestall extinction. In contrast to traditional theory in conservation biology, which attempts to separate ecological from evolutionary factors in the risk of population extinction, the Evolutionary Conservation Biology activity within IIASA's Adaptive Dynamics Network (ADN) project aims at developing integrated models to account for the feedback loop that links ecological and evolutionary factors as determinants of population dynamics and viability.

As environmental conditions change, they challenge individuals by creating new selective pressures to which their life-history traits must adapt. These life-history adaptive dynamics in turn have an impact on population dynamics and become a potentially important component of the population's risk of extinction. ADN's theoretical approaches demonstrate that these adaptive responses to threats can have positive as well as negative effects on population viability. The effect critically depends on the types of environmental changes encountered and how they alter the different life-history stages of the species under consideration. ADN's findings convey an essential message to wildlife managers: conservation planning requires that critical elements of the ecological–evolutionary feedback loop be identified, protected, and perhaps restored if attempts to preserve a substantial fraction of existing biodiversity are to have any lasting effect.

Experimental Evidence for Rapid, Adaptive Life-History Changes

One traditionally thinks of evolution as operating on such a slow time scale (e.g., the geological time scale used by paleontologists) that it should interact only negligibly with ecological processes. Yet several recent observational and experimental studies—including research on Hawaiian mosquitofish, German blackcaps, Galapagos finches, Trinidad guppies, and Bahamian lizards—provide clear demonstrations of extremely fast adaptive responses of morphological and life-history traits to environmental change.

Figure 1: Guppies are ideal for experimentally probing adaptive life-history responses to environmental perturbations.

Probably the most striking experimental results were obtained by ADN collaborator David Reznick of the University of California, Riverside, and his colleagues, who worked on natural populations of guppies (Figure 1). In 1976, they transferred guppies (*Poecilia reticulata*) from a high-predation site (inhabited by the perch-like species *Crenicichla alta*) in the Aripo River, Trinidad, to a low-predation site (*C. alta* absent) in the same river. In 1981, Reznick made a similar transplant in the El Cedro River, Trinidad. Subsequent sampling revealed that guppies in the new populations matured later and at a larger size, and produced smaller broods. The researchers were able to measure the genetic component of the change in these characters and came to the convincing conclusion that significant genetic divergence had occurred in the predicted direction after only 11 years in the Aripo River and after 8 years in the El Cedro River. Changes in such basic life-history traits as age and size at maturity and fecundity have a direct impact on population dynamics, and Reznick's experiments provide very strong support for the contention that environmental change can have major effects on population persistence through the adaptive responses of individual traits.

Adaptive Dynamics in Communities: From Population Self-Extinction to Evolutionary Insurance

Adaptive dynamics theory shows that evolution by natural selection does not necessarily entail an ultimate increase in any measure of population wealth, such as population size. A primary implication is that, even in a constant environment, there is no reason to think that adaptive change always enhances population viability.

Several of IIASA's ADN research activities have illustrated this point. In predator–prey systems, adaptive traits such as average individual body size respond to the selective pressure imposed by the other, interacting species. On an ecological time scale, these traits influence the dynamics of both populations, and beyond certain threshold values either population may become nonviable. Simple models show that under certain environmental conditions the adaptive dynamics of the traits drive the system across these thresholds and eventually doom the interaction either to dissolution (the predator goes extinct and only the prey population remains) or to complete extinction. In other words, evolution can cause self-extinction.

Similar phenomena have recently been found in models of the adaptive dynamics of mutualisms. Mutualisms, such as symbiotic interactions between plants and fungi, are of critical importance in the functioning of many ecosystems and have recently been shown to be a major determinant of biodiversity (Figure 2). This raises an intriguing puzzle: how can mutualisms be so widespread and of such great

Figure 2: A small bee provides pollination services to a barrel cactus in the Sonoran desert. The bee receives nectar as a reward. Natural selection has molded this kind of mutualistic interaction to resist dissolution or extinction potentially caused by "cheaters" that reap the mutualistic commodities without providing much benefit in return.

importance in the whole history of life, given that they seem highly vulnerable to "cheaters," that is, conspecifics or members of other species that skim off the commodities traded between partners without providing any benefit in return?

Answers to this question are important for conserving biodiversity in natural communities threatened by the disruption of interactions through direct impact on member species or indirect effects of invasive species. Recent ADN work shows that mutualistic associations evolve only under stringent conditions, yet evolved mutualisms develop significant resistance to environmental perturbations that might give rise to a risk of exploitation, or even extinction. Indeed, mutualisms demonstrate a natural tendency to diversify through the internal evolution of individual morphs that develop cheating behaviors. The cost imposed by such cheaters turns out to be balanced by the concomitant evolution of other individual types that are better mutualists than their ancestors. This combination of self-evolved cheaters and better mutualists endows the association with a form of flexibility that may allow it to sustain the assault of exploiters. In light of these results, it is tempting to infer that older mutualistic associations may have developed a kind of evolutionary insurance against even severe environmental changes that involve species deletions and invasions of their net of interactions.

Figure 3: Habitat fragmentation: A satellite photo of the Amazonian rainforest in Brazil shows the impact of a major highway. Roads leading from the highway into the forest in turn give rise to secondary and tertiary paths that fragment the forest into small, irregular patches. For species inhabiting this area, fragmentation induces new selective pressures on individual mobility traits such as natal dispersal; in response, the adaptive dynamics of such traits influence the risk of population extinction.

Adaptive Responses to Habitat Degradation

Human population growth and economic activity convert vast natural areas for settlement, agriculture, and forestry. This leads to such ecological effects as habitat destruction, degradation, and fragmentation, among the most important causes of species decline and biodiversity loss (Figure 3). For example, habitat destruction contributes to the extinction risk of three-quarters of the threatened mammals of Australasia and the Americas, and more than half the world's endangered birds. Populations facing local degradation of their environment can react evolutionarily in basically two ways: by locally adapting to the new environmental conditions, or by evolving dispersal adaptations that may allow individuals to shift their spatial range efficiently in search of locally better habitats.

Several ADN studies are currently exploring the consequences of these double-sided responses for the viability of populations affected by increasingly fragmented and/or locally altered habitat. In this context, ADN models a population as a set of patches, each containing a finite number of individuals. Such a population, made up of several (often many) small subpopulations is called a metapopulation. Individuals may disperse at birth or stay in their natal patch. The negative effects that local crowding exerts on birth and survival rates regulate the populations within a patch.

Empirical and theoretical ecologists have scrutinized metapopulation functioning for several decades, but only recently have appropriate mathematical tools become available for analyzing their dynamical properties. Such theoretical insights are anxiously awaited by wildlife conservation organizations endeavoring to protect the remnant metapopulations of threatened species. For example, the Orsini's viper, *Vipera ursinii* (Figure 4), a small insectivorous snake, has become the most endangered reptile in Europe because logging, the development of tourist activities, and intensive agricultural practices have led to the rapid fragmentation and destruction of its fragile grassland habitat. Field studies of this snake's demography and genetics are currently under way in France and Hungary. We are developing models that integrate these data to test how different management options that act upon ecological and evolutionary factors may enhance the long-term viability of *V. ursinii*.

On the theoretical side, IIASA's ADN project has developed rigorous measures of fitness (the long-term growth rate of a population in a given environment) that allow scientists to study the effects of individual factors on the long-term adaptive dynamics of a particular metapopulation. Using these new concepts, ADN has produced analytically tractable ecological metapopulation models that incorporate both individual parameters and environmental characteristics.

Figure 4: The Orsini's viper, *Vipera ursinii*, is now recognized as the most endangered reptile in Europe due to the rapid deterioration of its grassland habitat. Long-term demographic and genetic studies are currently under way in France and Hungary, on the basis of which IIASA's ADN project is developing detailed population models taking ecological and evolutionary factors into account in order to assess alternative management programs.

Researchers apply these models to predict the evolutionary dynamics of the metapopulation, focusing in particular on the evolution of dispersal rates. Dynamical systems theory then provides the mathematical means (bifurcation analysis) to construct exhaustive classifications of evolutionary outcomes for different environmental conditions. This makes it possible to understand how the evolutionary process and different regimes of environmental changes may interact to determine short-term metapopulation dynamics and viability. For instance, the results could indicate those changes that might jeopardize viability through evolutionary effects, such as the self-extinction described above, as well as changes that might contribute to a population's long-term survival.

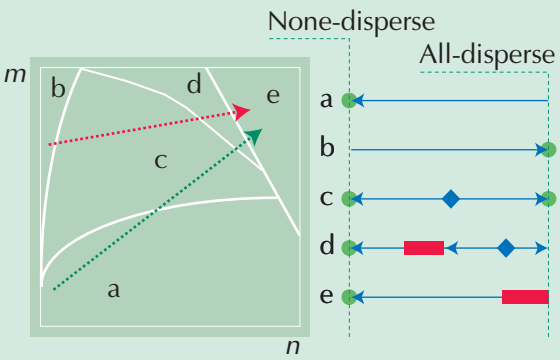
Metapopulation Adaptive Dynamics: Rescue and Suicide

The figure on page 16 provides an example of how ADN's theory operates. The goal is to characterize the dispersal trait value favored by natural selection under various environmental conditions. We assume that degrading environmental conditions increase the mortality rates of all individuals and promote extra mortality among those individuals that channel energy away from their own survival requirements to equipping their offspring with dispersal structures (such as structures that aid airborne dispersal, e.g., tufts or "wings" on seeds). As a result of this trade-off, the more likely it is that the offspring will disperse, the higher the mortality rate of the parents.

The figure shows how the adaptive dynamics of dispersal and corresponding metapopulation viability respond to such impacts of environmental change. Two contrasting cases emerge. In one case, evolution favors the non-dispersal strategy under the ancestral, presumably favorable, environmental conditions. As the habitat deteriorates (dotted green arrow in the figure), a transitional phase occurs in the evolutionary history of the metapopulation during which natural selection could also promote another dispersal strategy ("all offspring disperse"). Chance and history decide which strategy will prevail in the population. But switching from the former "none-disperse" strategy to the latter "all-disperse" strategy would require very unlikely random events, such as macromutations, that exert large effects on the individuals' dispersal probability. Thus, notwithstanding this evolutionary alternative, the metapopulation remains fixed at the ancestral strategy—much to its ecological safety! Indeed, in the long run, as the habitat undergoes further deterioration, the alternative strategy, although favored by natural selection among many other strategies, would not allow the population to persist: at the individual level (the level at which natural selection acts), the strategy is advantageous; but at the population level, it has the devastating effect of producing unavoidable extinction. In a sense, the adaptive dynamics of individual dispersal, which keep promoting the most viable dispersal strategy, "rescue" the metapopulation from an increasing risk of extinction.

In sharp contrast, a slight difference in the impact of environmental change on mortality parameters (dotted red arrow in the figure) may have vastly different consequences for dispersal adaptation and metapopulation viability. In this case, ancestral adaptation that took place when environmental conditions were at their best put an "all-disperse" strategy in place in the metapopulation. As before, at a certain stage of environmental degradation the same two alternative adaptive responses become available; but again, unless macromutations occur, the metapopulation will retain its ancestral strategy. This, however, turns out to be a suicidal response to the continued habitat destruction for the metapopulation as a whole. The all-disperse strategy does not remain viable under further environmental deterioration, and thus the metapopulation becomes caught in an evolutionary trap created by selective pressures, whereas the alternative strategy could, in principle, offer an ecologically safer option.

This brief overview should suffice to show that adaptive dynamics can have direct and profound effects on metapopulation viability. Whether these effects benefit or harm species persistence critically depends on how changes in environmental conditions target the different components of the species' life-history.



Adaptive response of dispersal to environmental degradation and consequences for metapopulation viability. Dispersal is an important adaptive, behavioral trait measured by the proportion of offspring that leave their natal site. Different dispersal strategies will evolve under different environmental conditions that are characterized by their effect on individual mortality (*m* parameter) and the additional mortality cost incurred by parents who produce dispersing offspring (*n* parameter). The left panel displays regions of the parameter space (*m*, *n*), as bounded by white curves, that correspond to different adaptive dynamics of the dispersal trait. These adaptive dynamics of dispersal are presented on the right (a to e). For any given value of *m* and *n*, there are two possible endpoints for the evolution of dispersal (green circles): the "none-disperse" strategy and the "all-disperse" strategy. In some cases (as shown in c), both strategies are attainable depending on whether the ancestral state is located on the left or on the right of an evolutionary repeller (blue diamond). Red areas indicate ranges of dispersal trait values that would condemn the metapopulation to extinction.

Arrows in the left panel indicate two hypothetical regimes of environmental change, both resulting in an increase of *m* and *n*. Although the two scenarios are not vastly different in terms of their effect on *m* and *n*, the adaptive response of dispersal has dramatically different consequences on metapopulation viability. Along the path indicated by the green arrow, evolution first drives dispersal to zero (a). Then an evolutionary repeller comes into play (c), coexisting with the alternative potential endpoint for the adaptive dynamics (all-disperse). As the environment continues to degrade, a range of nonviable dispersal probabilities arises (d). But the none-disperse strategy is still favored (e), which ensures maximum metapopulation viability. Along the red arrow, the adaptive dynamics initially promote maximum dispersal (b). In response to environmental change, as indicated by the red arrow, the evolutionary repeller and the alternative evolutionary endpoint (none-disperse) appear (c). Then the range of nonviable dispersal probabilities develops (d) and ends up "absorbing" the all-disperse strategy at which the population has been maintained by the adaptive dynamics (e): evolutionary suicide occurs.

Conclusion

Evolutionary conservation biology seeks to answer a question that has become increasingly urgent as human activities alter the natural environment: Can populations or species adapt rapidly enough to new, deteriorated conditions to avoid extinction? This question has opened a new avenue of population modeling that aims at combining ecological and evolutionary factors to predict the short-term viability of specific populations and the outcome of long-term processes that structure communities and generate diversity.

IIASA's ADN project intends to play a leading role in fostering these novel directions of research. In addition to driving the necessary mathematical and conceptual developments that evolutionary conservation biology requires, and working with specialists in the field, ADN collaborates with social scientists, economists, and environmental managers to translate its research findings into policy guidance. In this way, ADN may play a helpful role in converting scientific knowledge into practical decisions that may counteract the constraints and, often, persistent antagonism of powerful political and economic interests.

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

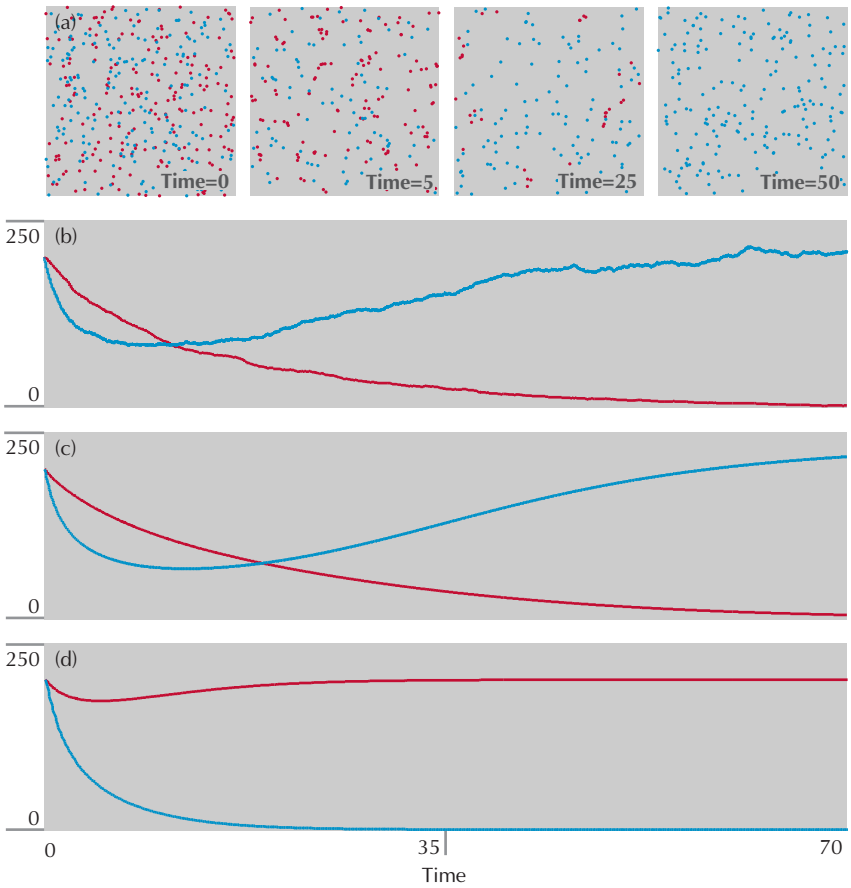
Simplifying Spatial Complexity

A sea change has come over theoretical ecology in the past 10 years. The heyday of the simple, general model that sought to capture the essence of an ecological community has passed. Today, ecological modeling relies on individual-based, spatially explicit computer simulations. Research has shown that spatial variations in population density within a given domain, both self-generated and exogenous, have major impacts on predictions of ecological and evolutionary change.

Individual-based simulations encompass the randomness of ecological dynamics that results from individual behavior and life-histories. Yet ecological researchers should not infer too much from single examples or simulations: it is not the location and behavior of each single individual that matters. Instead, to understand the relevance of pattern and process in spatial ecology, we must ask: What spatial and temporal patterns develop in the long run? How can they be characterized? Can we identify different kinds of patterns developing as the initial configuration of an ecological community changes? How many different kinds of patterns are expected to develop from different starting conditions? What happens when the environment in which the organisms live is altered, thus affecting the parameters of the ecological process? These are important questions, but ones that are very difficult to answer from examining instances of an individual-based process.

Along with a few other groups around the world (in Princeton, USA, and in Fukuoka, Japan), IIASA's ADN project is developing novel methods that provide answers to these questions. Mathematical techniques, including pair approximations and correlation dynamics, allow ADN to predict the changing spatial statistics of an individual-based process in terms of relatively simple deterministic models (see figure below). By analyzing these models, ADN can deal with many of the issues left unresolved by both the traditional nonspatial models of population ecology and by the modern generation of individual-based simulations.

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



Correlation dynamics succeed in simplifying spatial complexity. (a) Changing patterns of two locally competing populations. One species (red) is the better competitor, the other (blue) the better disperser. (b) Over time, the better disperser wins, driving the better competitor to extinction. (c) The new correlation dynamics developed by IIASA's ADN project correctly capture this behavior of the complex spatial model. (d) In contrast, traditional nonspatial population models perform poorly on the same task: their forecasts predict the extinction of the better disperser, a qualitative error.

Evolution of Cooperation

The evolution of cooperation presents a major problem in theoretical biology, because helping others may impose a cost on the helper. It is therefore not immediately obvious how cooperation can persist. Supposedly, cooperative interactions originated through two primary mechanisms: kin selection (readiness to assist biological relatives) and reciprocal altruism. The latter is likely to arise if the same two individuals meet repeatedly and can exchange acts of assistance. This mechanism has been studied intensively. However, another form of reciprocation may also take place even if the same two players never meet a second time. This mechanism, called indirect reciprocity, may have played a critical role in the evolution of hominid and human societies.

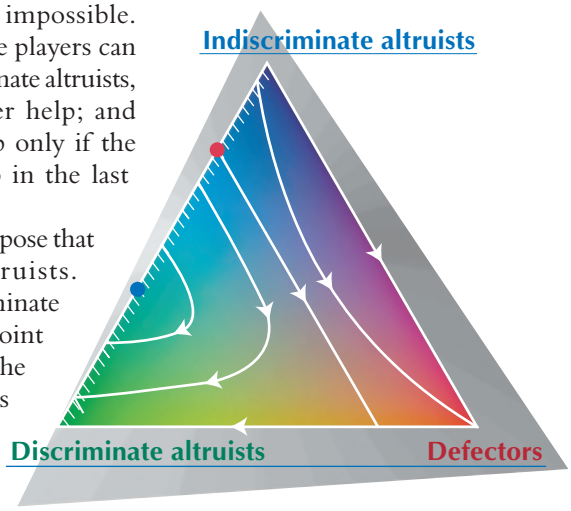
The paper "Evolution of Indirect Reciprocity by Image Scoring," by Martin A. Nowak and Karl Sigmund (*Nature* **393**; 11 June, 1998) highlighted the importance of indirect reciprocity for maintaining cooperation. For a complete list of ADN publications on this topic, visit the IIASA ADN Web page www.iiasa.ac.at/Research/ADN/Cooperation.html.

To test this theory, ADN recently developed a model for the evolution of indirect reciprocity. Although the actual model is quite complex, a simplified and analytically tractable version reveals its essentials. In this model, each player has two interactions per round, one as a donor and one as a recipient. The same two individuals are never paired twice and direct reciprocation is thus impossible. Depending on the strategies they use, the players can fall into one of three categories: indiscriminate altruists, who always help; defectors, who never help; and discriminate altruists, who provide help only if the potential recipient itself has given help in the last round.

This leads to interesting behavior. Suppose that the society consists entirely of altruists. Depending on the frequency of discriminate altruists, its composition is given by a point along the hatched edge in the figure to the right. We can expect that random drift lets the state fluctuate along this edge and that, from time to time, mutations introduce a small quantity of defectors.

What happens? If the state is above the red point, the defectors will take over. If it is below the blue point, defectors will immediately be selected against and will promptly vanish. But if a minority of defectors invades while the state is between the red and blue points, then defectors will at first exploit the indiscriminate altruists and will increase in frequency. Thereby, however, they will deplete their resource (the indiscriminate altruists), and eventually the discriminate altruists will take over and eliminate the defectors. The population will thus return to the hatched edge, but now to a state somewhere below the blue point. In this way, the defectors will have experienced a Pyrrhic victory. They can only hope that fluctuations will eventually decrease the frequency of discriminate altruists again. To succeed, the defectors must wait until the population's composition has moved above the red point. This requires that fluctuations cross the gap between the blue and the red points, which takes considerable time.

Therefore, if defectors try to invade too often, they will never succeed. In other words, cooperation can persist in populations that are challenged by defectors sufficiently often. ADN's research thus provides a rigorous basis for the viewpoint that societies may actually benefit from a certain level of stress.



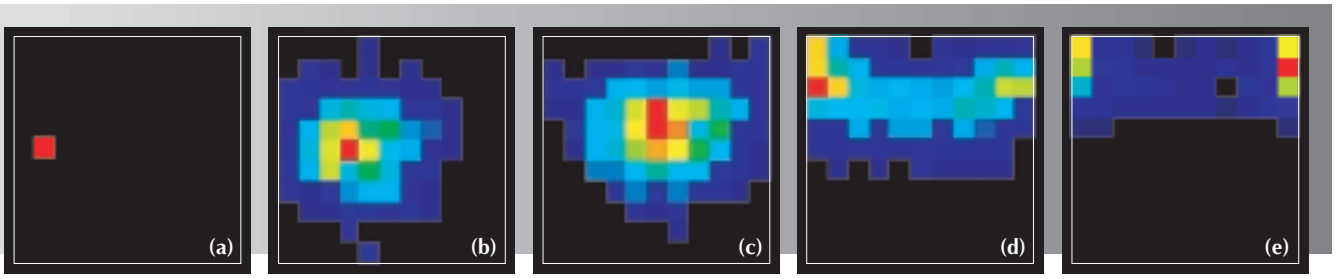
Adaptive Speciation

Conventional wisdom holds that new species primarily arise from a common ancestor when populations become isolated geographically—a process known as allopatric ("other homeland") speciation. Yet empirical evidence, based on recent studies of various species of plants and animals, indicates that new species can also occur as a result of sympatric ("same homeland") speciation, where subpopulations that no longer look alike or mate with each other appear within a single geographic habitat.

Research by IIASA's ADN project has strengthened the theoretical foundation for sympatric speciation by incorporating population genetics and mating mechanisms into ecological models. ADN's models show that situations in which individuals must compete for resources can often select against the predominant type and lead to selective mating. When individuals mate primarily with others like themselves, a sexually reproducing population can split into two subspecies. Over multiple generations, these subspecies cease to mate with each other, and their genetic makeup diverges. Such evolutionary branching can occur either if the mating choice depends on a trait directly related to fitness in the environment, such as body size or temperature preference, or if it is based on a selectively neutral trait, such as coloration or courtship behavior. In the former case (see figure below), however, scientists predict that speciation will proceed more rapidly.

The recent paper "On the Origin of Species by Sympatric Speciation," by Ulf Dieckmann and Michael Doebeli (*Nature* **400**; 22 July, 1999) attracted considerable attention among geneticists and ecologists. ADN's 1999 workshop, held at IIASA, focused on "The Formation of Biodiversity through Adaptive Speciation"; the papers presented at the meeting will serve as the basis of the fifth volume in the *Cambridge Studies in Adaptive Dynamics* series. For a complete list of ADN publications on this topic, visit the IIASA ADN Web page www.iiasa.ac.at/Research/ADN/Speciation.html.

ADN's findings hold for wide ranges of competitive interactions and have also been demonstrated to apply to all other fundamental types of ecological interaction. Other researchers confirm that ADN's approach solves problems that have undercut other models of disruptive selection. These results could change the way scientists view the generation of biodiversity by speciation processes—a topic still vigorously debated 140 years after Charles Darwin's groundbreaking treatise *On the Origin of Species* appeared in 1859.



Evolutionary branching can lead to sympatric speciation in sexual populations. Loci in this individual-based multi-locus model are diploid, diallelic, and additive, and recombine freely. The five figures show the evolution of the frequency distribution of phenotypes (from high to low: red, orange, yellow, green, cyan, blue, black) for two metric traits: an ecological character (horizontal) and a second character that determines type and degree of assortative mating (vertical: upper half = assortative; lower half = disassortative). (a) Evolution starts from a randomly mating population; (b) directional selection drives the population toward an evolutionary branching point located at the center of the horizontal axis; (c) disruptive selection at the branching point induces increased degrees of assortative mating; (d) after this increase, disruptive selection can split the phenotypic distribution into two branches; ultimately (e) gene flow between the two branches essentially ceases.

Evolutionary Algorithms

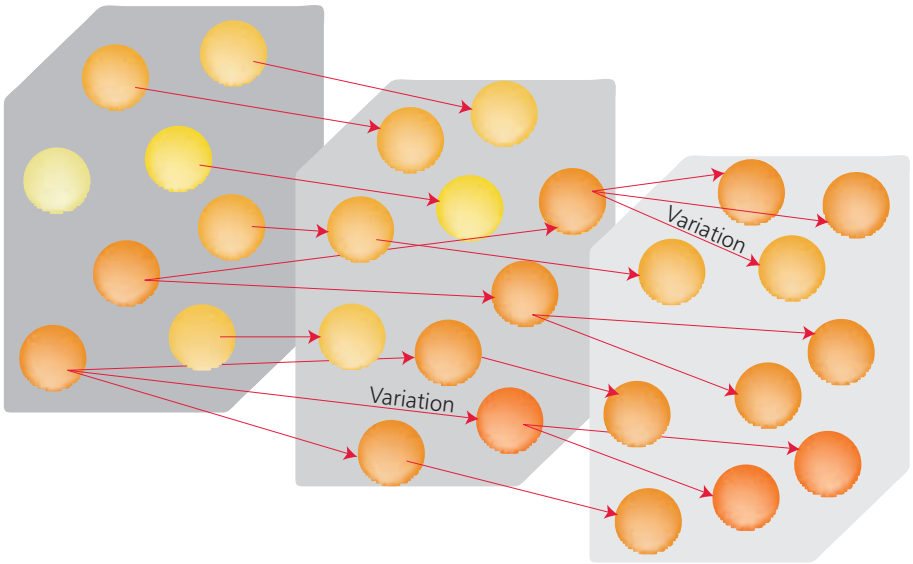


Figure 1: Evolutionary problem solving. Solutions to a computational problem are represented as individuals of a population *(left)*. The better a solution (from light yellow to dark orange), the higher its chance of contributing offspring to the next generation of the population *(center)*. Offspring solutions can contain slight variations relative to their parents; these variations are highlighted above. Gradually, good solutions are bound to accumulate in the population *(right)*.

Evolutionary algorithms utilize the principles of biological evolution to solve computational problems. Such algorithms are based on a "population" of potential solutions; these solutions "reproduce" with some variation according to their quality (Figure 1) so that the resulting population will produce continually improving solutions. For problems in which the space of potential solutions is very large, evolutionary algorithms can often achieve excellent results (see Figures 2 and 3).

Although evolutionary algorithms offer an appealing general-purpose toolbox for solving complex computational problems, and therefore have become more and more important in commercial and industrial applications, their inner workings are still only poorly understood. IIASA's ADN project is developing methods for analyzing the dynamics of such algorithms within the very high-dimensional search spaces in which they are set to operate. Results of this research allow for a better understanding of complex evolutionary processes in general and of the expected performance of evolutionary algorithms on specific problems in particular.

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

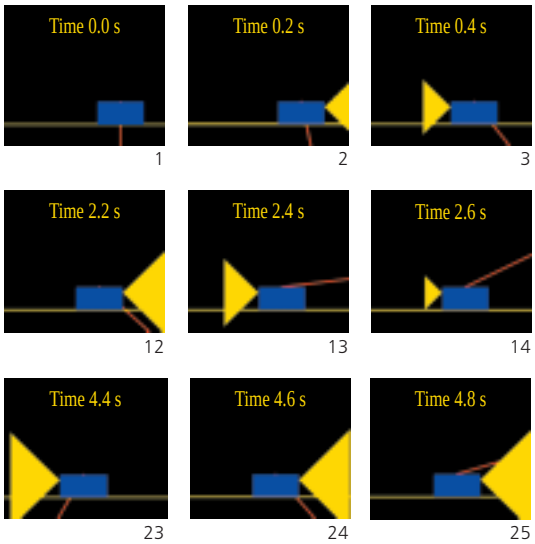


Figure 3: An evolutionary algorithm has automatically constructed a controller that brings a pendulum (red), mounted with a joint onto a cart (blue), into an upright position and keeps it balanced by moving the cart along a horizontal track (yellow). The forces exerted by the evolved controller are indicated by yellow triangles.

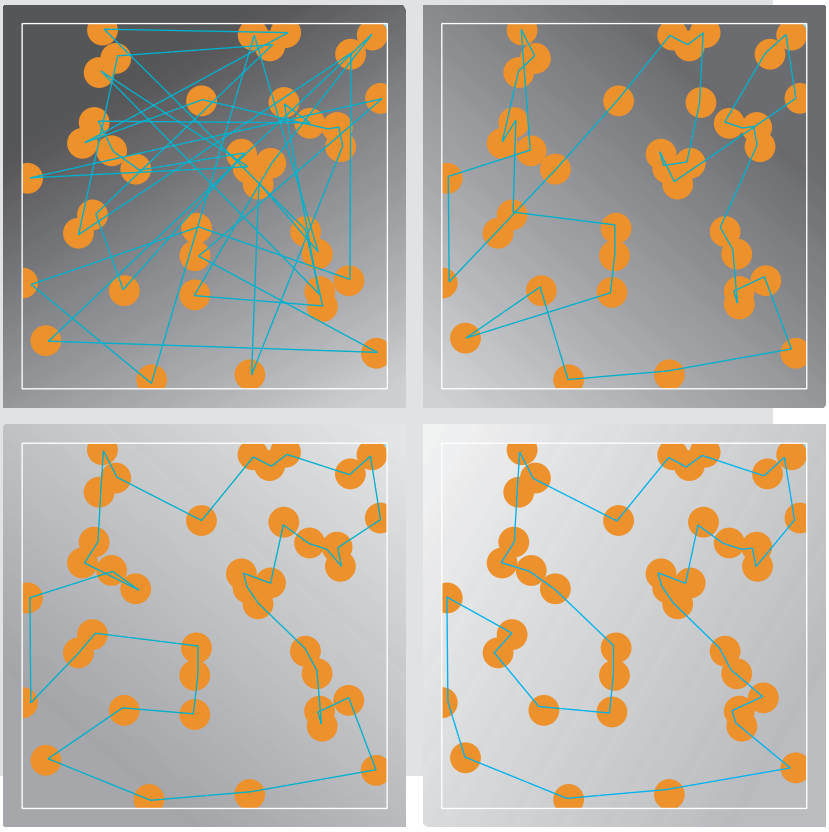
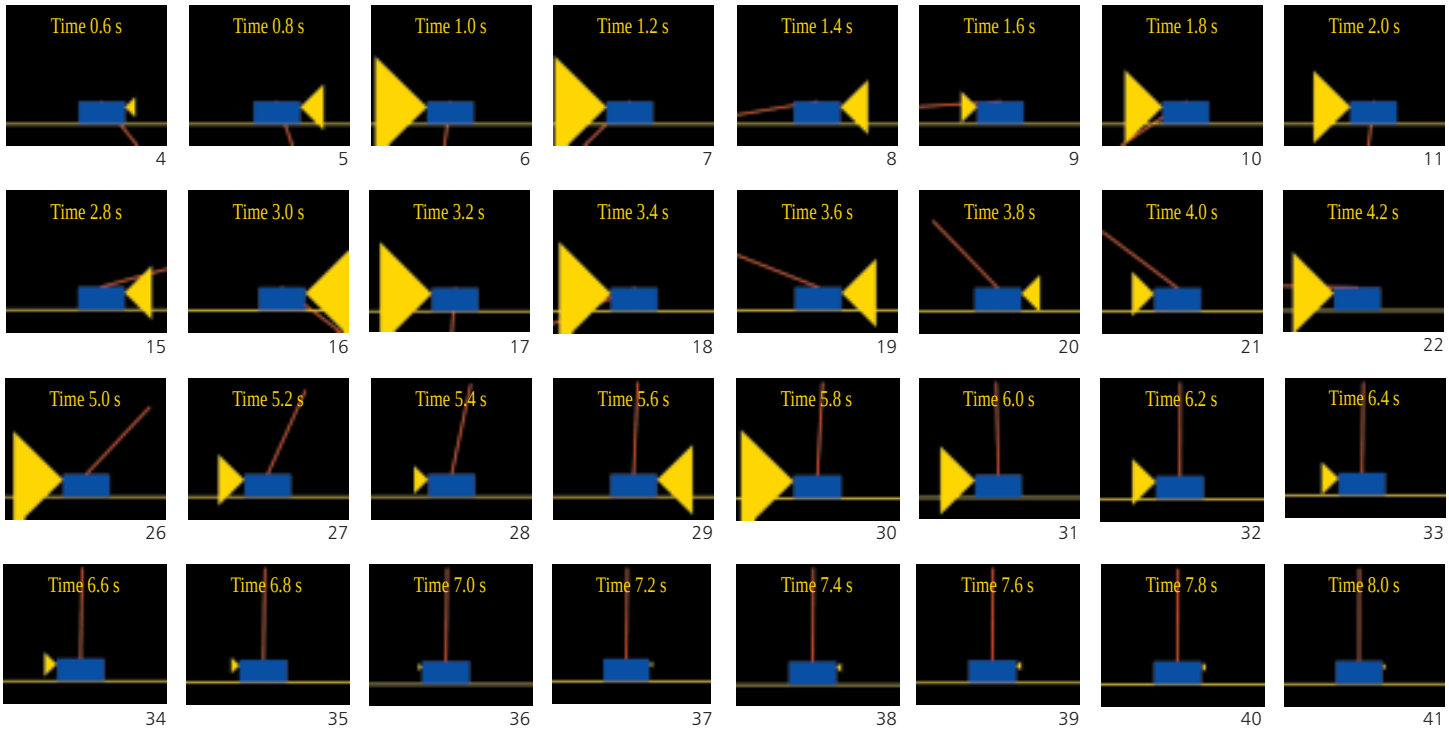


Figure 2: An evolutionary algorithm solves the Traveling Salesman Problem by finding one of the shortest itineraries through a given set of cities.



Adaptive Dynamics Network Web Page

IIASA's Adaptive Dynamics Network (ADN) project maintains an extensive Web page within IIASA's Web site—www.iiasa.ac.at/Research/ADN. The page provides interested researchers an entry point to information about ongoing and planned activities, as well as links to related sites. The contents are grouped under four main headings:

- *Project* encompasses items describing ADN's overall mission and research goals. It details the specific research interests of staff members and gives contact information.
- *Service* presents features useful to researchers studying the adaptive changes in the Earth's biotic environment. Among other items, this portion of the Web page contains a full electronic version of Charles Darwin's *On the Origin of Species* and a list of the most influential journals related to ADN's fields of interest, weighted according to their impact factors. It also describes various capabilities still under development, including online tours and tutorials on adaptive dynamics, and a software tool known as the Adaptive Dynamics Integrated Simulation Environment (ADISE). This package will allow users to specify an ecological environment and the species that inhabit it, and then apply adaptive dynamics methods to examine the course and outcome of potential evolutionary changes.
- *Network* gives users access to information about past and future ADN workshops and project collaborators in 15 countries. It highlights ADN's commitment to student involvement and contains links to electronic versions of all ADN Interim Reports on adaptive dynamics. Most of these reports are published in the refereed journal literature.
- *Research* introduces each of the main themes of ADN's work through summaries and graphic illustrations. Each description features a list of ADN publications related to that topic.

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ModLife: A European Research Training Network

IIASA's Adaptive Dynamics Network (ADN) coordinates the European Research Training Network *ModLife*. Titled *Modern Life-History Theory and its Application to the Management of Natural Resources*, research in this network aims at enhancing understanding of life-history adaptations to imposed environmental threats and in realistic ecological settings. Starting in September 2000 and running for a duration of 3½ years, this European Commission funded network brings together six research teams from five countries.

Seven postdoctoral positions are currently available within the ModLife network, each for a duration of up to 2 years and 8 months:

Population Biologist
Statistical analysis of life-history changes in selected fish stocks
Adaptive Dynamics Network, IIASA, Austria

Theoretical Biologist / Biomathematician
Modeling life-history change in exploited populations
Adaptive Dynamics Network, IIASA, Austria

Population Biologist / Biomathematician
Modeling phenotypic plasticity in exploited fish populations
Institute of Marine Research, Bergen, Norway

Theoretical Biologist / Biomathematician
Density-dependent life-history theory
Institute of Evolutionary and Ecological Sciences, Leiden University, The Netherlands

Population Biologist / Biomathematician
Life-history adaptive responses to environmental change
École Normale Supérieure, Paris, France

Biomathematician
Adaptive metapopulation dynamics
Department of Mathematical Sciences, University of Turku, Finland

Population Biologist
Colonization, invasion, and the evolution of dispersal
Laboratoire d'Écologie, Université Pierre et Marie Curie, Paris, France

For details about these vacancies and for information on how to apply, see IIASA's ADN Web page www.iiasa.ac.at/Research/ADN/ModLife.

IIASA Conference Honors Winfried Lang

Approximately 60 dignitaries and academicians gathered at IIASA on 25 February 2000 to honor the memory of Winfried Lang (1941–1999), an Austrian career diplomat, professor of international law and international relations at the University of Vienna, and specialist in international negotiation. Ambassador Lang had served as a prominent member of IIASA's Processes of International Negotiation (PIN) project since its inception in 1988. The Winfried Lang Memorial Conference received financial support from the Austrian Federal Ministry for Education, Science and Culture.

The meeting themes highlighted the combination of research and practical applications in key areas of Winfried Lang's scientific interests. Ambassador Hans Winkler, head of the International Law Department of the Austrian Federal Ministry for Foreign Affairs, delivered the keynote address, which focused on the milestones of Ambassador Lang's career and his role in strengthening linkages between law and diplomacy, and between science and the real world. Alois Mock, former foreign minister and vice-chancellor of Austria, Franz Cede, currently Austria's ambassador to Russia, and I. William Zartman, distinguished professor at the School of Advanced International Studies, Johns Hopkins University, also presented tributes to their late friend and colleague.

Following these talks, the PIN Steering Committee held a panel discussion in which each speaker highlighted a different aspect of Ambassador Lang's areas of interest and related it to ongoing work in the study of negotiation. The panelists were Rudolf Avenhaus, University of the Bundeswehr, Munich; Guy Olivier Faure, Sorbonne University, Paris; Victor Kremenyuk, Russian Academy of Sciences, Moscow; Paul Meerts, Clingendael Institute, The Hague; Gunnar Sjöstedt, Swedish Institute of International Affairs, Stockholm; and I. William Zartman. The conference concluded with a personal reminiscence by Matthias Lang, son of the late ambassador, in which he characterized his family as a solar system, with his father as a brilliant comet who brought illumination from the diverse spheres through which he traveled.

Winfried Lang served as Austria's ambassador to the international organizations in Geneva (1993–1996) and to Belgium (1997–1999). He chaired the Organisation for Economic Co-operation and Development's Transfrontier Pollution Group from 1977–1982, and presided over UN conferences on the protection of the ozone layer (1985), on biological and bacteriological weapons (1986), and on substances that deplete the ozone layer (1987). During the negotiations on the General Agreement on Tariffs and Trade, Lang arbitrated a trade and environment dispute between the United States and the European Union. From 1993 until his death, he served as a member of the Board of Trustees of the UN Institute for Training and Research. Lang also published several books and articles on integration policy, protection of the environment, international negotiations, neutrality, and the law of treaties.

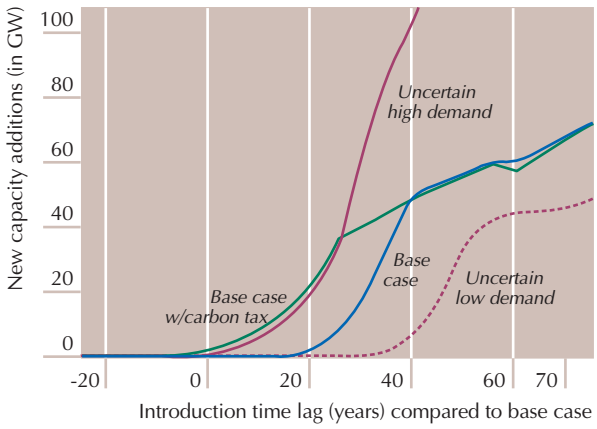
Top left: Alois Mock with Gordon J. MacDonald. Bottom left: Adam Michel, Austria's ambassador to Belgium, with Franz Cede. Above: I. William Zartman with Matthias Lang.

Improving Prediction of Technology Diffusion

During the past decade, researchers at IIASA have examined and modeled the processes that govern the introduction, diffusion, and widespread adoption of new energy technologies. A key challenge has been to devise ways of incorporating technological choices and technology development as intrinsic components of models used to project economic and environmental futures.

Currently, the technology scenarios developed with mainstream models often depend on questionable assumptions, such as "oil prices will rise continuously because resources are finite," or arbitrary input assumptions, such as "by 2025, biomass power plants will be 25 percent more efficient than they are today." Yet a review of the historical record reveals that the introduction and diffusion of technologies in competitive markets follow characteristic patterns, trajectories, and time scales. They reflect cost reductions and performance improvements resulting from technological learning, regular patterns of dynamic competition among different approaches to a given problem, and the coevolution of long-lived infrastructures and technology clusters.

IIASA researchers have generated mathematical representations of these learning curves and incorporated them into microscale models as simple quantified characterizations of likely improvements in cost and performance of energy technologies as a result of cumulative experience and investments. The models can accommodate not only the S-shaped diffusion patterns and time scales of technological dynamics, but also the uncertainty that stems from "surprises," such as the appearance of radically new technologies. Research has also identified early indicators of the particular startup technologies that will be selected for investment and development, and therefore have a chance to become widespread. The study suggests that creative scenarios could accommodate not only when a new technology might appear, but also when and how it could become accepted as part of the mix of mainstream technologies.



Endogenous technological change with carbon constraints and other uncertainties. Figure shows new capacity additions for three model simulation runs: (1) base case (blue) with cost improvements due to uncertain rates of learning (possibilities for future cost reductions); (2) addition of an uncertain carbon constraint (green); and (3) addition of the possibility that demand for electricity will be substantially higher (red) or lower (dashed red) than expected in the base case simulation. Source: Grübler, A. and Gritsevskii, A., A Model of Endogenous Technological Change through Uncertain Returns on Learning (R&D and Investments), *Ukrainian Economic Review*, V(7) (forthcoming).

IIASA researchers have also succeeded in including learning phenomena statistically in macroscale models of the world energy system. In fact, model runs have yielded projections indicating the possibility of reducing environmental impacts without harming economic growth. However, achieving such a result in the long term depends on policy interventions, such as incentives to promote greater diversity of technology and lower barriers to entry for new infrastructures that could accelerate historical trends of decarbonization.

One surprising, and encouraging, result identified a historically robust trend toward greater carbon and energy efficiency in the world economy. Modern infrastructures that replace long-lived systems tend to be powered by energy sources that yield progressively more energy per unit of carbon pollution. This process, driven primarily by economic incentives, now "decarbonizes" the global economy by 1.3 percent per year without deliberate action by government or industry—a trend that most baseline projections for carbon emissions ignore.

This IIASA study provides guidelines that can lead to substantial improvement in the models of technological change used for policy analysis. An article titled "Dynamics of Energy Technologies and Global Change," by Arnulf Grübler, Nebojša Nakićenović, and David Victor (*Energy Policy* **27**:247–280) describes the research and offers detailed recommendations regarding modeling and scenario writing. The article is also available from IIASA as Research Report RR-99-007.

For more information, contact:
Nebojša Nakićenović (E-mail: naki@iiasa.ac.at)
Arnulf Grübler (E-mail: gruebler@iiasa.ac.at)

Russia: Regional Differences May Promote Fragmentation

Many Russian factories that formerly received government subsidies have fallen into disrepair. The loss of modern industrial capacity contributes to the decline of Russia's economy.

As background to its ongoing study of the institutional framework of the Russian forest sector, IIASA's Forestry (FOR) project examined the effects of Russia's economic restructuring on industrial output and efficiency in the period from 1987 to 1997. The analysis drew on source data produced by Russia's national statistical bureau, including figures on earnings, employment, and capital, and on industrial output. For each of 89 regions, FOR correlated indicators of industrial structure with output decline. The project also estimated the common Cobb-Douglas production function over all regions and industries to identify the changing contributions of labor and capital to output, and to estimate economies of scale in production.

Not surprisingly, FOR's research showed that both the efficiency and the productivity of the Russian economy as a whole decreased significantly from 1987 to 1997. The study also revealed striking variations among the subjects of the Russian Federation. For example, those regions that host a variety of industries and small, localized enterprises fared better than those dominated by a single commercial sector or gigantic production facilities. The most successful regions, many of which gained their income primarily from resource extraction, more than doubled their revenues over the period studied. By contrast, the least successful regions—most of them dependent on agriculture, machine building, light industry, and the traditional chemical industry—saw their incomes shrink to approximately a third of 1987 levels. The trend toward the economic dominance of resource-extractive industries increased over the study period, reinforced by the cost-effective production methods of its associated processing industries, which took advantage of economies of scale.

Based on these findings, IIASA's FOR project reached the sobering conclusion that regional economic disparities could accelerate the fragmentation of the Russian Federation. As wealth becomes ever more concentrated in parts of the country with large—and nontransferable—resources of metals and fuel, these areas may increasingly come into conflict with the central government over royalty policies and revenue transfers to poorer regions. Ethnic tensions between Russians and non-Russians could further heighten such disputes. To counteract further national disintegration, the study recommends that Russia's national government, as well as the international lending community, target their policies specifically toward supporting the development of manufacturing and services enterprises. These sectors are especially well suited to benefit from the talents of Russia's highly educated population, and they depend upon openness, knowledge transfer, and cooperation rather than on natural resources. Such an emphasis would not only increase the country's overall revenue, but would also contribute to cohesion by spreading economic gains more equally throughout the Federation. The study points out, however, that such a restructuring program can only come about from strong institutional embedding of dedicated and targeted reforms, as well as appropriate macroeconomic and trade policies.

Restructuring, Efficiency and Output Decline of Russian Industries and Regions, by Michael Obersteiner (IIASA Interim Report IR-99-066; November 1999), describes the study in detail and suggests explanations for the outcomes of Russia's failed restructuring efforts. FOR has also published other reports that provide detailed information on the institutions governing the forest sector in eight Russian regions, as well as more general overviews of the country's legislative structure as it relates to the forests. Full text of these papers can be viewed on IIASA's Web site at www.iiasa.ac.at.

For more information, contact:
Sten Nilsson (E-mail: nilsson@iiasa.ac.at)

Awards and Recognition

Ambassador Lars Björkbom, chairman of the Convention on Long-Range Transboundary Air Pollution (LRTAP) Working Group on Strategies, singled out Markus Amann, leader of IIASA's Transboundary Air Pollution project, for special recognition in the official presentation of the draft Protocol to Abate Acidification, Eutrophication and Ground-level Ozone, on 30 November 1999. Björkbom's transmittal letter stated, "There have of course been a number of key persons. . .who have played particularly significant roles in sustaining the [LRTAP] process over the years. . . . I can't name them all, but in the context of the present protocol, I think the name of *one* person should be mentioned. It is Dr. Markus Amann from IIASA. I can assure you that without his constructive role and the enormous workload that he has carried over the last five years, you would have had neither a multipollutant nor a multi-effects protocol to adopt and sign."

♦♦♦♦♦

Two IIASA scientists recently have been habilitated by Austrian universities. Ulf Dieckmann, project coordinator of IIASA's Adaptive Dynamics Network, was granted the habilitation in biomathematics by The University of Vienna, where he has taught courses on evolutionary theory and biomathematics. Arnulf Grübler, research scholar with IIASA's Transition to New Technologies activity, received the habilitation in systems science of environment and technology from the University of Leoben, where he teaches a regular course on technology and environment.

A habilitation, or *venia legendi*, entitles the holder to supervise students' master and doctoral dissertations and to carry the title Univ.Doz (Universitätsdozent).

IIASA Establishes Raiffa Scholarship

On 4 April 2000, Professor Howard Raiffa, the Institute's first director, received the 1999 Dickson Prize for Science and generously donated a portion of his prize money to IIASA. The Dickson Prize, conferred every year by Carnegie Mellon University, honors individuals who have made outstanding contributions to science. Raiffa is credited with introducing game theory to many social scientists and with launching the new scholarly field of decision sciences. Raiffa's selection for the lifetime achievement award is especially notable because he is the first scientist in a nontraditional field to receive the honor.

The Raiffa Scholarship will be awarded annually to a student in IIASA's Young Scientists Summer Program (YSSP) participating in the Processes of International Negotiation (PIN) project. PIN's mission is to improve the process and understanding of negotiation—an endeavor important to Raiffa throughout his career.

Raiffa, currently the Frank Plumpton Ramsey Professor of Managerial Economics, Emeritus, at Harvard Business School, was a key negotiator with leaders of the United States, Russia, and other world powers in the formation of IIASA and establishment of its charter in 1972.

IIASA Inaugurates Activity on Technological Innovation

At the end of January 2000, IIASA initiated a new research activity on Transitions to New Technologies (TNT) to focus on a broad range of new and emerging technologies that have the potential to transform society, including emerging capabilities in the fields of information, communication, and transportation, as well as in energy production and end-use. The new activity builds on the long tradition of technology research at IIASA that started virtually with the inception of the Institute. By collaborating closely with other IIASA research activities, TNT aims also to foster research on the technology dimension of other developments investigated at IIASA. In particular, the new activity will analyze possible diffusion patterns and interlinkages of cutting-edge technologies, as well as their potential economic, social, and environmental impacts that may result from their widespread adoption. In this context, TNT will investigate how various combinations of new technologies might fundamentally affect human activities, and the institutional and organizational changes that would result.

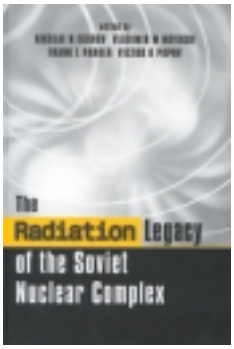
IIASA's TNT activities fall into three categories: "Diffusion of New Technologies," "Modeling Adoption of New Technologies," and "Combinations of New Technologies." To study diffusion, TNT will examine and document historical patterns of technological change, including the associated infrastructure and institutional prerequisites for rapid adoption of new technologies, incentives and barriers to innovation, and environmental implications. The results can provide insight into possible future patterns of technical innovation and diffusion. In the modeling area, researchers will develop new methods to capture the dynamics of technological change in time and space, including efforts to develop an operational multi-agent, multi-region model with endogenous technological change reflecting economic uncertainty, increasing returns, and environmental externalities. Finally, TNT will construct "future case studies" to help examine synergies among innovations, as well as their interactions with new institutional and infrastructural developments. The findings may indicate ways in which new technologies could transform and change human activities in general.

For further information on TNT, contact:
Nebojša Nakićenović (E-mail: naki@iiasa.ac.at)

Recent Publications

The Radiation Legacy of the Soviet Nuclear Complex

In March 2000, Earthscan Publications, in association with IIASA, published *The Radiation Legacy of the Soviet Nuclear Complex*. The book represents a collaboration between IIASA's Radiation Safety of the Biosphere (RAD) project and Russian scientists from institutions of the Ministry of Atomic Energy of the Russian Federation (Minatom), the Russian Academy of Sciences, and the Russian Research Center "Kurchatov Institute." It provides the first authoritative and detailed information available outside the former Soviet Union regarding the nuclear inheritance of the past half century and allows scientists to compare the quantities of radioactive materials produced in the West with those produced in the East. Among other data, the book gives the location and characteristics of the accumulated radioactive material and wastes according to each stage of the production process, from ore and mining to use and disposal. It also gives details on the territories and locations contaminated by normal operations and by accidents—information that can serve as a basis for formulating strategic plans for remediation.



The book has already received considerable attention in Russia. RAD project staff presented findings from the book and its other studies at a press conference held in Moscow at the end of February; the event was covered in a Russian television news program and in five articles in the Russian print media. In a meeting with RAD Project Co-Leader Vladimir Novikov, Dr. Vladimir Grachev, chairman of the Committee on Ecology of the Parliament of the Russian Federation, stated that he considers the book an important reference for work on new legislative acts and standards dealing with nuclear developments in Russia. IIASA has already received requests for translations from English into Russian and Chinese. Project Co-Leader Frank Parker wrote an article on this topic for the *Financial Times*.

The Radiation Legacy of the Soviet Nuclear Complex is edited by Nikolai N. Egorov, former deputy minister in Minatom; Vladimir M. Novikov and Frank L. Parker, co-leaders of the RAD project; and Victor K. Popov, head of the Laboratory of Information Analytical Studies at the Kurchatov Institute.

E-mail earthinfo@earthscan.co.uk for ordering information. ISBN 1 85383 658 3 • Price: £50.

Macroeconomic Developments in the Candidate Countries with Respect to the Accession Process

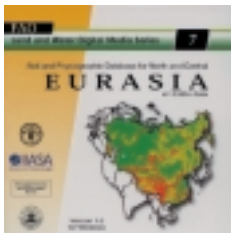
As 10 transition countries prepare for membership in the European Union (EU), the EU has funded a comprehensive international research project called PREPARITY to study the likely impact of the accession process on current EU states adjacent to the candidate countries. The Austrian Institute of Economic Research (WIFO), which manages Austria's research for PREPARITY, chose IIASA's Economic Transition and Integration (ETI) project to examine the expected macroeconomic development of the 10 East European candidate countries, with especially detailed analysis devoted to Poland, the Czech Republic, Slovakia, Hungary, and Slovenia. In March WIFO published the summary study resulting from ETI's research: *Macroeconomic Developments in the Candidate Countries with Respect to the Accession Process*.

In conducting this research, IIASA's ETI project developed scenarios showing that a pending, announced accession in 2005 would moderately accelerate economic development in the candidate countries even before the accession occurs, largely because of the lower perceived financial risks. The difference between the two development scenarios analyzed—accession in 2005 and no accession before 2010—becomes more pronounced starting in 2005, when each country's gross domestic product would grow by an additional 1 percent or more annually in the case of accession as opposed to non-accession.

IIASA's ETI project has already received a strongly positive response to its study, both within WIFO and at the international workshops of the PREPARITY project, where Project Leader János Gács presented the results in November. For information on ordering the full report, or to view summaries in English and German, see the PREPARITY Web site at preparity.wsr.ac.at/public/ergebnisse. ETI also published five IIASA Interim Reports that describe the country case studies and environmental protection costs that served as the basis of the summary report; these are available in hard copy or can be downloaded from IIASA's Publications Web page www.iiasa.ac.at/Publications.

IIASA Releases CD-ROMs on Land and Land Use

In cooperation with the Food and Agriculture Organization of the United Nations (FAO), IIASA has released two new CD-ROMs. The first, "Soil and Physiographic Database for North and Central Eurasia," updates the FAO *Soil Map of the World*. The CD, the first of its kind to include detailed information on Russia, also provides data on all countries of the former Soviet Union, as well as on China and Mongolia, all at a 1:5 million scale.



IIASA prepared this database as part of a larger FAO program, supported by a number of international institutes and organizations such as the United Nations Environment Programme, the International Soil Reference and Information Centre, and the European Soil Bureau. The soil information was derived from several sources, in particular the *Soil Map of the Former Soviet Union* (formally known as the *Soil Map of the Russian Soviet Federative Socialist Republic*) at scale 1:2.5 million, prepared by the Dokuchaev Institute, Moscow, and the *Soil Map of China* at scale 1:4 million, prepared by the Soil Science Institute of the Academia Sinica in Nanjing. Coordinated by Vladimir Stolbovoi (formerly with IIASA's Land-Use [LUC] project, now with its Forestry project), LUC staff put considerable effort into checking, correcting, and linking digital data received from the FAO and other collaborating organizations, and ensuring that the data were mutually consistent. LUC also contributed a series of its own digital databases that could be applied for a number of other specific analyses by the national and international scientific community.

The second CD-ROM, "AEZWIN: An Interactive Multiple-Criteria Analysis Tool for Land Resources Appraisal," provides a Windows application of the FAO Agro-Ecological Zones (AEZ) methodology. The software package is a specialized tool intended primarily to support land resources appraisal for land-use planning and management, and for teaching and research regarding AEZ. Both IIASA's LUC project and its Risk, Modeling and Society (RMS) project contributed to developing this software package.

The AEZWIN software, developed by LUC Project Leader Günther Fischer, Marek Makowski of RMS, and IIASA collaborator Janusz Granat (Warsaw University of Technology), features modules for data management, land suitability and land productivity assessment, and multi-criteria model analysis (MCMA) tools for land-use optimization, and draws upon examples from a national AEZ study of Kenya. The software makes it possible to generate models interactively that correspond to various scenarios of land use and then to analyze these models using the MCMA approach. A user-friendly interface with an online tutorial permits even people with limited computer experience to use the software.

Both CD-ROMs are available from the FAO; for ordering information, see IIASA's LUC Web page www.iiasa.ac.at/Research/LUC.

New Staff at IIASA

Staff Member	Project	Country
Erika Alfaro Gallaga	Institute Scholars (Colosio Fellow)	Mexico
John Casti*	General Research (GEN)	USA
Martijn Egas*	Adaptive Dynamics Network (ADN)	Netherlands
Mary Ellen Gallagher	Office of Information	USA
Karen Gerwitz	Office of Information	USA
Klaus Hubacek*	Modeling Land-Use and Land-Cover Changes in Europe and Northern Asia (LUC)	Austria
Walid Khalifa	Modeling Land-Use and Land-Cover Changes in Europe and Northern Asia (LUC)	Egypt
Atsutoshi Makihira	Environmentally Compatible Energy Strategies (ECS)	Japan
Soili Nysten-Haarala	Forestry (FOR)	Finland
Makoto Takano	Radiation Safety of the Biosphere (RAD)	Japan

*Returning staff member

In Memoriam

Professor Ferenc Rabár, who led IIASA's Food and Agriculture program from 1975 to 1980 and again from 1985 to 1987, died on 29 December 1999. Professor Rabár, who lectured on economics at universities around the world and authored many books and articles on micro- and macroeconomic planning and modeling, served as finance minister of the first democratically elected Hungarian government from 1990 to 1993.

IIASA's ADN Project Initiates Book Series
Cambridge Studies in Adaptive Dynamics

An initiative by IIASA's Adaptive Dynamics Network (ADN) project has led to a new book series, the *Cambridge Studies in Adaptive Dynamics*. That Cambridge University Press, a highly respected scientific publisher, has undertaken to produce this series demonstrates the growing recognition among scientists that the emerging adaptive dynamics framework constitutes a critical step forward in explaining, understanding, and predicting the interplay between ecological and evolutionary phenomena in the biological realm.

The books of this series are specifically designed to help graduate students and researchers in biology, ecology, and genetics apply this innovative approach to their own studies. Because of the wide relevance of adaptive processes, the target audience extends well beyond this core group to include physicists, mathematicians, and computer scientists.

Cambridge University Press launched the series with the May 2000 publication of *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*, edited by Ulf Dieckmann, Richard Law, and Johan A.J. Metz. Ordering information for this book appears overleaf. The next two volumes currently in preparation are

- *The Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, edited by Ulf Dieckmann, Johan A.J. Metz, Maurice Sabelis, and Karl Sigmund
- *Elements of Adaptive Dynamics*, edited by Ulf Dieckmann and Johan A.J. Metz

ADN staff members Ulf Dieckmann and Johan Metz, who serve as series editors, and Cambridge University Press invite researchers to contribute ideas and manuscripts for this series. For more information, see IIASA's ADN Web page www.iiasa.ac.at/Research/ADN/Books.html.

The Geometry of Ecological Interactions

Simplifying Spatial Complexity

Edited by U. Dieckmann, R. Law, and J.A.J. Metz

The field of spatial ecology has expanded dramatically in the past few years. This volume, written by world experts in the field, gives detailed coverage of the main areas of development in spatial ecological theory. Integrating a perspective from field ecology with novel methods for simplifying spatial complexity, it offers a didactical treatment with a gradual increase in mathematical sophistication. In addition, the volume features introductions to those fundamental phenomena in spatial ecology where emerging spatial patterns influence ecological outcomes qualitatively as well as quantitatively. An appreciation and understanding of such systematic departures from standard, nonspatial models is required if ecological theory is to move on in the 21st century. Written for graduate students and researchers in theoretical, evolutionary and spatial ecology, applied mathematics, and spatial statistics, this book is a ground-breaking treatment of modern spatial ecological theory.

Ulf Dieckmann is Project Coordinator of the Adaptive Dynamics Network at the International Institute for Applied Systems Analysis (IIASA) in Laxenburg, Austria.

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The Geometry of Ecological Interactions

Simplifying Spatial Complexity

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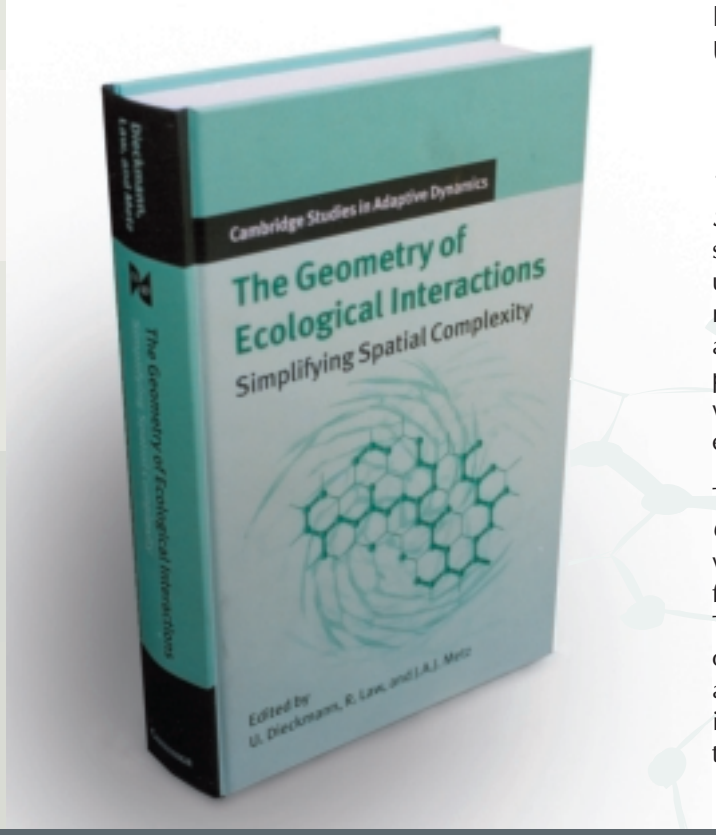
"Timely! Dealing with topics that have become the leading edge of ecology in the last ten years."

C.S. Holling
Department of Zoology
University of Florida, USA

"The editors of this book have contributions from the best-known experts in the field of spatial complexity—every chapter has something to give the ecologist."

Mats Gyllenberg
Department of Mathematics
University of Turku, Finland



The Geometry of Ecological Interactions: Simplifying Spatial Complexity helps scientists and the enlightened lay reader understand the spatial complexity of real ecological systems. The book offers an innovative perspective that links patterns and processes in the natural world. A must for students of ecology, evolution, and mathematics.

This volume, the first in the series *Cambridge Studies in Adaptive Dynamics*, was produced by the International Institute for Applied Systems Analysis (IIASA). The Cambridge series enhances understanding of biological adaptive phenomena through a mathematical and statistics approach incorporating empirical observations and theoretical insights.

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