Evolution and Ecology Program

Research Plan for 2006-2010

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Evolution is the architect and custodian of all biological diversity. Insights about the dynamics of adaptation are thus indispensable for understanding the past, present, and future of Earth's ecosystems. If human interventions directed at responsible conservation and sustainable exploitation are to be successful, they must account for the evolutionary dimensions of anthropogenic environmental change. Responding to this increasingly recognized need, IIASA's Evolution and Ecology Program analyzes and forecasts how evolutionary dynamics shape ecological populations and communities. Specific challenges addressed range from assessing and managing human-induced evolutionary changes in exploited fish stocks, to fostering cooperation in groups of unrelated agents, to understanding and forecasting the impact of environmental disturbances on the structure and functioning of food webs. Together with its network of international collaborators, the Program is driving the development and application of adaptive dynamics theory, a framework recognized by many as the most versatile tool currently available for linking ecological and evolutionary consequences of environmental change. Based on a two-pronged attack through applied and methodological research, the Program establishes bridges between fundamental and policy-oriented, theoretical and empirical, biological and mathematical, and analytical and numerical approaches to the systems analysis of ecological and evolutionary change.

Introduction

As anthropogenic damage to the Earth's biota spans unprecedented temporal and spatial scales (Millenium Ecosystem Assessment 2005), the close interaction between ecological and evolutionary processes in shaping the properties of ecosystems can no longer be ignored. Until recently, however, ecological processes have typically been analyzed assuming evolutionary stasis (e.g., Yoshida et al. 2003), and evolutionary processes have often been modeled without accounting for their ecological embedding (e.g., Dieckmann and Ferrière 2004). Two misunderstandings, in particular, have been widespread. First, human-induced evolutionary processes have been believed to be so slow that purely ecological considerations were deemed sufficient for guiding conservation policies or strategies for the sustainable exploitation of living natural resources. By contrast, evidence for rapid contemporary evolutionary change has been mounting: ecologically salient properties of species can evolve over just one or two decades, and sometimes even within a few years (Zimmer 2003). Second, evolutionary processes are still expected invariably to benefit the evolving species. The counterintuitive fact that (under conditions technically known as frequency-dependent selection) evolution can worsen a population's lot has been, and oftentimes still is, left out of consideration (Matsuda and Abrams 1994; Ferrière 2000; Gyllenberg et al. 2004). These observations imply the need for a fundamental reappraisal of the role evolution plays in the interaction of humans with their biotic environment (Palumbi 2002; Stockwell and Ashley 2004).

The Evolution and Ecology Program at IIASA contributes to defining and driving the resultant research agenda at an international level, highlighting the importance of evolution for various policy-relevant questions of global concern and developing innovative methods and

tools for meeting the new challenges. Over the next few years, the Program plans to concentrate its research activities on four projects, taking advantage of proven strengths and addressing a suite of timely issues:

- *Project 1: Adaptive Dynamics Theory.* The Program will seek to advance IIASA's unique role as the major driving force behind the development and application of adaptive dynamics theory, which offers versatile methods for addressing the eco-evolutionary implications of environmental change.

- *Project 2: Evolutionary Fisheries Management.* Tackling a problem of considerable socio-economic consequence, the Program will work on developing the foundations of applied evolutionary fisheries science, by devising suitable case studies and models and by advising policy-makers and resource managers as to how undesired fisheries-induced evolution can be avoided or reversed.

- *Project 3: Evolution of Cooperation.* The Program will continue developing its research into the evolution of cooperation, with the aim of delivering comprehensive insights into measures and settings that can be expected to prevent selfish behavior from jeopardizing shared interests within groups of individuals.

- *Project 4: Evolving Biodiversity.* Opening up new ground in biodiversity science, the Program will investigate the evolutionary determinants of ecosystem structure and functioning, and further the scientific understanding of the evolutionary responses of entire food webs to environmental disturbances including harvesting.

These individual research projects have been selected and designed so as to generate a dense web of interconnected activities, with three strategic goals in mind. First, the combination of the four projects outlined above will perpetuate at IIASA a highly stimulating intellectual atmosphere that can be trusted to keep attracting an international community of promising young researchers and distinguished scientists. Second, the chosen targets exemplify the range of qualitatively different contributions ecological science can make toward the solution of pressing global problems – from innovative policy advice for the evolutionarily enlightened management of living natural resources, to general insights into how cooperation is fostered over selfishness, to the breaking of new ground by elucidating evolutionary responses at the level of ecological communities. Third, the planned mix of targets and methods is geared to continue the successful stream of scientific publications in the Program's subject area that has enhanced IIASA's international visibility over the past few years.

Ecology has a long history at IIASA, with successful and internationally recognized activities going almost as far back as the Institute's foundation. One reason for the persistent role of ecology in IIASA's research is that analyzing biotic changes in ignorance of ecological and evolutionary processes offers only limited insights. Another reason is that ecological research embodies a strong tradition of methodological pluralism, enabling the field to take best advantage of the breadth of established and emerging tools of modern systems analysis. The interdisciplinary nature of ecological theory – with contributions coming from various areas of biology, as well as from mathematics, physics, and computer science – matches IIASA's profile. The Evolution and Ecology Program is also well embedded in a potent network of international collaborators, multiplying the Program's impact and guaranteeing the effective dissemination of findings obtained at IIASA. Finally, given the high propensity of ecological protection in general and fisheries policies in particular to conflict with sensitive national interests, IIASA's role as an independent and unbiased source of scientific insights serves a helpful asset for the Program's successful operation.

The synergies between the strategic advantages of IIASA-based research are particularly evident in the Program's research on evolutionary fisheries management. In this area, the work

carried out at IIASA has successfully overcome a history of stagnation that had already lasted for decades. Such a development was possible because of several key characteristics of IIASA's research:

- IIASA's work can readily transcend long-established disciplinary divides – in this case by building sound bridges between stock assessment science and life-history theory.

- The approaches taken are likely to enhance traditional methodology with fresh perspectives from modern systems analysis – which resulted in the development of novel statistical tools and innovative dynamical models for the analysis and management of stock dynamics.

- IIASA's infrastructure can provide a sufficiently stable research platform – which proved vital during the years it took for moving the Program's ground-laying work on fisheries-induced evolution to a publication in *Nature*.

- The Program's activities are capitalizing on IIASA's well-established instruments for global networking – involving international workshops, inter-institutional agreements, local capacity building, and collaborative research organized around accompanying book projects.

- The Institute strongly benefits from its international standing as a scientific agency independent of national interests – which facilitated overcoming local traditions and reservations that sometimes constrict the free flow of scientific information and ideas in fisheries science.

Except for the last aspect, which is of special importance for fisheries research, these considerations apply to all projects to be carried out by the Program. For example, IIASA's stable involvement has enabled the Institute to become recognized as a global player in studying the evolution of cooperation; evolutionary analyses of food web structure and functioning are deriving new perspectives from merging traditions alternatively rooted in population ecology and evolutionary ecology; and the development of adaptive dynamics theory greatly benefits from the strong and persistent international collaborations for which IIASA is rightfully famous.

Background

Evolution and ecology govern the properties of ecosystems, with ecological dynamics determining aspects like abundances and spatial composition, and evolutionary dynamics controlling features like traits and genetic composition. The Program's research agenda is driven by the realization that in many problems of global concern ecological and evolutionary dynamics are inextricably intertwined (e.g., Yoshida et al. 2003; Ferrière et al. 2004). On the one hand, adaptive traits determine the conditions under which ecological dynamics unfold, and thus affect abundances. On the other hand, with natural selection aptly characterized as ecology in action, the dynamics of abundances naturally underlie the dynamics of traits. This mutual dependence is captured by the so-called eco-evolutionary feedback loop (Metz et al. 1992; Dieckmann and Ferrière 2004), which lies at the heart of most of the Program's research (for an overview see Dieckmann and Metz 2000). It is only in recent years that this feedback is increasingly appreciated as being ubiquitous in natural systems. Applied problems for which eco-evolutionary feedback is decisive are legion and range from the conservation of species and ecosystems to the management of living resources and societal interactions, to the harnessing of biological processes for agricultural or medical needs.

Project 1: Adaptive Dynamics Theory

Given the pervasiveness of eco-evolutionary feedback, it is surprising that analyses of its implications have been (and, some would argue, still are) relatively scarce. Eco-evolutionary feedback is relevant whenever selection is frequency-dependent. This applies when selection pressures depend on the phenotypic composition of a population, a situation that turns out to be the rule in natural systems. Until recently, yet, no methodological framework was available for investigating frequency-dependent selection in a conceptually unified, ecologically realistic, and technically versatile manner. This lacuna has been filled by the development of adaptive dynamics theory (Metz et al. 1992, 1996a; Dieckmann and Law 1996; Geritz et al. 1997, 1998). IIASA has played a key role in establishing the foundations as well as many applications of this theory.

Only a few years ago, the common wisdom in evolutionary ecology was that adaptive evolution would optimize a population's phenotypic state in the sense of maximizing some suitably chosen measure of fitness, such as a population's density, its intrinsic growth rate r, or its basic reproduction ratio R_0 (Roughgarden 1979; Stearns 1992; Roff 1992). On this basis it was largely expected that adaptive evolutionary change would always enhance population viability. In fact, such confidence in the prowess of adaptive evolution goes back as far as Darwin, who suggested that "Natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each" (Darwin 1859).

Despite repeated discussions about the limitations of optimizing selection (e.g., Lewontin 1979, 1987; Emlen 1987), it is remarkable how long it has taken researchers to account for these. One reason for this slow progress is that seminal approaches to evolutionary theory had favored the idea of evolution as an optimizing process. First, following a notion introduced by Wright (1932), adaptive evolution was often envisaged as a hill-climbing process on a fixed fitness landscape. Second, a similar idea underpins Fisher's so-called "fundamental theorem of natural selection" (Fisher 1930), which predicts mean population fitness to increase monotonically over the course of adaptive evolution – provided, however, that certain restrictive assumptions are fulfilled. It is not surprising that one of these assumptions is the constancy of fitness values, and thus the absence of frequency-dependent selection (Roughgarden 1979; Frank and Slatkin 1992). Also the fitness-set approach by Levins (1962a, 1962b, 1968), enjoying widespread recognition in teaching and research (Yodzis 1989; Calow 1999; Case 1999), is based on the assumption that, within a set of feasible phenotypes defined by a trade-off, evolution maximizes fitness. Fourth, even though Roughgarden (1979) tackled evolution on dynamic fitness landscapes, his approach of evolutionarily maximizing a population's density is applicable only when selection is merely density-dependent, and not when it is frequency-dependent – which still left out the majority of ecologically realistic settings. Fifth, the concept of frequency-dependent selection continues to receive short shrift in contemporary textbooks on life-history evolution. For example, out of the close to 500 pages of Roff (2002), not more than five deal with the description and implications of frequency-dependent selection, while the corresponding percentages in another seminal textbook of life-history evolution (Stearns 1992) – or in textbooks of genetics – are even smaller.

Capitalizing on the pioneering work on evolutionary game theory (Maynard Smith 1982), the past decade of research has finally done away with viewing life-history evolution as a simple optimizing process. First, it was realized that any optimization principles driving the evolution of life histories could and should be derived from the population dynamics that underlie the process of adaptation (Metz et al. 1992, 1996a; Dieckmann 1994; Dieckmann et al. 1995; Ferrière and Gatto 1995; Dieckmann and Law 1996). In the wake of this insight, the old debate as to whether r or R_0 was the more appropriate measure of fitness (e.g., Stearns 1992; Roff 1992) became largely obliterated (Pásztor et al. 1996). Second, it is now understood that the particular way in which population densities and traits overlap in their impact on the dynamics of

evolving populations determines whether an optimization principle applies, and, if so, what specific fitness measure it ought to be based on (Mylius and Diekmann 1995; Metz et al. 1996b). It thus turned out that for many evolving systems no optimization principle exists and that the conditions that actually allow predicting life-history evolution by maximizing r or R_0 are very restricted (e.g., Meszéna et al. 2001; Dieckmann 2002). Third, it became clear that, even when adaptive evolution did optimize, the process would not necessarily maximize a population's viability (Matsuda and Abrams 1994; Ferrière 2000; Gyllenberg et al. 2002).

Tackling these various challenges, adaptive dynamics theory provides methods for identifying optimization principles when these exist, for predicting the course and outcome of evolution also in the absence of optimization principles, as well as for assessing the impact of evolutionary change on population viability. Accordingly, the fundamental features of adaptive dynamics theory, as outlined above, impinge on all of the Program's research efforts. Today, IIASA is perceived internationally as an important center of adaptive dynamics research: the next round of efforts at IIASA can capitalize on this position. A main thrust for the future will come from methodological integration, combining the strengths of adaptive dynamics theory with those of other approaches.

Project 2: Evolutionary Fisheries Management

By facilitating the evolutionarily responsible management of living marine resources, the Program targets a major gap in current fisheries science and management (Browman 2000; Conover 2000; Law 2000; Stokes and Law 2000; Kenchington and Heino 2002; Conover and Munch 2002; ICES 2002; Ashley et al. 2003). While the possibility of fisheries-induced evolutionary changes in exploited fish stocks has sporadically been acknowledged (mostly by scientists outside the fisheries community), evolutionary considerations failed for a long time to provoke an adequate response in the practice of fishery management (Brisov 1978; Edley and Law 1988; Law and Grey 1989; Sutherland 1990; Law 1991; Rijnsdorp 1993; Stokes et al. 1993). This oversight persisted despite the fact that, if some genetic variation allows individuals to increase their contribution to the next generation, either by adjusting their life cycle so as to reproduce as much as possible before getting fished or by decreasing their likelihood of being captured, then the corresponding genotypes will tend to increase in relative numbers. Downplaying the importance of such evolutionary changes has been particularly troublesome since these changes are likely to impact stock attributes of direct concern for fisheries management, such as sustainable yield and recruitment, as well as stock stability and recovery potential. In addition, evolutionary changes may be so slow to revert that great care should be taken not to induce them in the first place (Dieckmann et al. 2002; Cookson 2004). Why then the historical inertia towards accounting for evolutionary effects in fisheries management?

Two misperceptions appear to have played a role. First, it is often supposed that evolution is not relevant at the timescales of fisheries management. Evolution, as still taught in many textbooks, is conceived as a slow process, taking place at geological rather contemporary timescales. If so, then clearly there is no need for considering evolutionary processes in fisheries management, in which even a decade is often considered a long time period. Recent research has, however, revealed that evolution regularly occurs on contemporary timescales, often within decades (for a review see Hendry and Kinnison 1999). Rapid evolution may take as diverse forms as adaptation to new environments after species introductions, emergence of pest and pathogen resistant to chemical agents used for controlling them, or development of heavy-metal tolerance in plants colonizing waste heaps from mining activities. Even though natural causes can trigger rapid evolution, many examples of contemporary evolution involve anthropogenic agents as the ultimate causes of evolutionary change. It appears therefore unwarranted, if not irresponsible, to ignore the possibility of contemporary fisheries-induced evolution.

Second, it is often assumed that observations pointing at fisheries-induced evolution can be explained by other mechanisms. For example, evolutionary theory predicts that elevated harvest mortality over the age range during which maturation is possible causes evolution toward earlier maturation, as such evolution improves an organism's chances of reproducing before being captured. Earlier maturation is exactly what has been observed in the large majority of exploited fish stocks for which appropriate data are available (Trippel 1995). However, a similar response may occur also because of the phenotypic plasticity of maturation (Rijnsdorp 1993; Ernande et al. 2003). Exploitation often results in more rapid individual growth, a phenomenon known as a compensatory growth response. This is because competition for resources is bound to diminish when stocks are fished down. It is well known that well-fed, fast-growing fish tend to mature at an earlier age than those with poorer growth. Until very recently, the community of fisheries scientists and managers appeared to have had concluded, at least implicitly, that this compensatory growth response suffices for explaining the declining trends in maturation ages observed for most stocks. Considering evolutionary mechanisms would thus seem dispensable. This position was maintained despite the virtual absence of quantitative attempts to assess whether the suggested explanation in terms of phenotypic plasticity was indeed sufficient. Systematic tests would have been important since the two potential explanations, based, in turn, on plastic and genetic changes, are not mutually exclusive, and thus need to be assessed quantitatively.

It is only lately that fisheries scientists and managers have changed their views about the relevance of fisheries-induced evolution – owing, to a large extent, to the activities carried out at IIASA. Especially after a publication in *Nature* (Olsen et al. 2004), the importance of evolutionary approaches to fisheries management is meeting with increasing international acceptance. IIASA is thus is in a good position to expand its pioneering research in this area. Within the next years, further empirical evidence and innovative management tools are expected to firmly establish evolutionary fisheries management in the responsible agencies around the world.

Project 3: Evolution of Cooperation

One of the main motivations for the development of evolutionary game theory and of adaptive dynamics theory has been the need for understanding the evolution of cooperation, especially among non-relatives. Game theory may be viewed as the ideal mathematical tool of methodological individualism: the attempt to explain social behavior by reducing it to the actions and motivations of individuals. This perspective has been central to the development of sociobiology (Wilson 1975) and evolutionary game theory (Maynard Smith 1982), and also serves as the foundation for experimental economics (e.g., Camerer 2003; Fehr and Fischbacher 2003). In all these settings, frequency-dependent selection is key to understanding the outcome of evolution: the payoff that a particular strategy (be it to cooperate or to defect) reaps crucially depends on the distribution of other strategies followed by the players any focal individual will interact with. This explains the great potential for applying adaptive dynamics theory to the evolution of cooperation: the new approach helps to investigate the evolution of continuous strategies based on realistically complex population dynamics, thus addressing problems to which evolutionary game theory is not ideally suited.

The great public interest in understanding the evolution of cooperation is attested by many articles in top-ranking journals like *Nature*, *Science*, and *Scientific American* (with several of these having been contributed by IIASA scientists). In particular, much recent attention has been directed at the evolution of cooperation in public goods games. Public goods are crucial, indeed defining, elements for every society: sheltering, foraging, hunting, or defense are often collective enterprises. In many such situations, it is possible that individuals profit from the public good without contributing to it in full measure. Such defectors do better than coopera-

tors, within every group. Selection should therefore eliminate the cooperators, and the public good should vanish. Economists, psychologists, and students of animal behavior have studied such situations in experiments with humans (e.g., Dawes 1980; Colman 1995; Kagel and Roth 1995). To give a simple example of a public goods game, each member of a group of six players (who do not know each other and will not meet again) is given ten dollars and offered the possibility to invest some part of the money in a common pool. The players are told that the experimenter will triple the total amount in the pool, and distribute it equally among all players, irrespective of their contributions. If all players contribute fully, each earns thirty dollars. Note that all contributors receive only half of their own investments. Hence players are tempted to withhold their contribution. But if all decline to contribute, there is no pool to share. Such a public goods game neatly captures the social dilemmas caused by the discrepancy between individual and social welfare (Binmore 1994).

Right from the beginning of IIASA's operation, game theory played a central role in the Institute's research agenda. Also, right from the beginning of evolutionary game dynamics, many scientists staying at IIASA for shorter or longer periods have contributed substantially. Some other global players in the field have been influenced by scientists working at IIASA. Given this long and successful history, IIASA is in an excellent position to contribute to this field, further advancing the science of cooperation. Within the next five years, a rounded-up theory of cooperation based on reciprocity (including indirect reciprocity and strong reciprocity, with the latter notion characterizing a player's willingness to exercise costly punishment) is likely to emerge from a synthesis of the current research. This could culminate in a monograph on the evolution of cooperation, and in a user-friendly set of online tools for conducting hands-on experimentation. It is expected that such a systematic and unified treatment at the interface of evolutionary biology (e.g., Maynard Smith and Szathmary 1997) and experimental economics (e.g., Camerer 2003) will greatly benefit both fields.

Project 4: Evolving Biodiversity

With direct observation or manipulation of biodiversity evolution rarely being feasible, models are playing a key role in characterizing the ecological, evolutionary, and environmental factors that cause the formation, maintenance, and loss of species. Recently developed theory facilitates such understanding at two different levels, addressing, respectively, the adaptive dynamics of populations and communities.

At the population level new insights have emerged into the evolutionary dynamics of biodiversity formation and loss. While classical speciation theory emphasized the role of geographic isolation in triggering diversification (Mayr 1963), modern approaches have revealed how selection pressures originating from local ecological interactions may drive surprisingly rapid adaptive radiations (Schluter 2000; Dieckmann et al. 2004). Likewise, current theory has uncovered the active role evolutionary dynamics may play in the loss of biodiversity: far from being a reliable agent of species preservation, natural selection itself may be the driver of species extinctions (Matsuda and Abrams 1994; Ferrière 2000; Gyllenberg et al. 2002).

At the community level, past theory had focused mainly on the implications of evolutionary change for the stability of pairwise interactions – between predators and their prey (e.g., Marrow et al. 1996; Abrams 2000; Doebeli and Dieckmann 2000; Dercole et al. 2003), or among mutualists (e.g., Brown and Vincent 1992; Law and Dieckmann 1998; Ferrière et al. 2002; Bronstein et al. 2004) and competitors (e.g., Abrams 1989; Law et al. 1997; Kisdi 1999). Today, the evolution and self-assembly of whole ecological communities and multi-species food webs is attracting mounting attention (e.g., McKane 2004). Models have demonstrated how evolutionary change triggered by anthropogenic impacts on a single species can lead to co-

evolutionary cascades, sending evolutionary ripple effects through entire ecological communities and resulting in species extinctions that must remain unexpected as long as the underlying coevolutionary dynamics are not appreciated (e.g., Bronstein et al. 2004).

The science of ecosystem evolution is still in the early stages of its development, and currently available models either lack in ecological or evolutionary realism (Drossel and McKane 2003). This gap in understanding also extends to aspects of more specific concern: for example, the evolutionary implications of harvesting for the structure and functioning of communities have hardly been investigated. In view of the prevalent political and scientific drive toward an ecosystem approach to natural resource management in general and to fisheries policy in particular, such enhanced scientific insights are urgently needed (Garcia et al. 2003).

Given the Program's expertise and its history of contribution to fundamental and applied problems in evolutionary ecology, speciation research, and coevolutionary dynamics, the planned work at the interface between evolutionary modeling and biodiversity science is a natural target for expanding the Program's scope. Work on the evolutionary self-assembly of ecological communities and on their evolutionary responses to harvesting appear to be particularly promising.

Strategic Goal and Objectives

The Program's overall goal is to develop and apply novel methods for understanding the dynamics of complex adaptive systems and for evaluating the ecological and evolutionary implications of environmental interference. Models of complex adaptive systems are playing a key role in characterizing the ecological, evolutionary, and environmental factors that foster the formation, maintenance, and loss of species. The Program's research agenda is driven by the understanding that insights into the eco-evolutionary processes relevant to global change are typically gained at local and regional scales, thus necessitating an integrative theoretical framework for identifying and tackling universal issues. For this purpose the Program builds on the strong record of research established by IIASA's Adaptive Dynamics Network Program. Another critical asset of the Program's operation is its well-established international network of scientific collaborations, which endows the jointly initiated activities with considerable more leverage and impact than a more localized pursuit could achieve.

Based on a two-pronged attack through applied and methodological research, the Program establishes bridges between fundamental and policy-oriented, theoretical and empirical, biological and mathematical, and analytical and numerical approaches to the systems analysis of ecological and evolutionary change. The Program's applied research highlights fundamental policy-related issues in need of evolutionary analysis. Topical themes addressed include the worldwide impact of fisheries, the long-term conservation of biological diversity, the establishment of sustainable cooperation between intrinsically selfish actors, as well as the emergence and evolution of infectious diseases. Complementing these activities, the Program's methodological research delivers innovative tools for evolutionary analysis. Adaptive dynamics theory, developed at IIASA in close collaboration with scientists worldwide, has been specifically devised to evaluate the evolutionary implications of environmental change in realistic ecological settings. Other approaches contributing to the Program's methodological breadth include individual-based models of complex adaptive systems, innovative methods for simplifying spatial complexity, a new generation of speciation models, novel techniques of dynamic programming, and eco-genetic models for examining the dynamics of evolving natural resources.

Implementation Plan

Research Framework

The pervasiveness of the eco-evolutionary feedback loop furnishes the Program's research agenda with a strong degree of conceptual integration. This integration, in turn, provides the basis for considerable mutual illumination between the different research projects laid out in this plan. In particular, research on the foundations and applications of adaptive dynamics theory provides the methodological backbone for most of the Program's scientific activities: therefore, general insights and novel tools derived from this core project can naturally be expected to have immediate applications in the other projects.

At the same time, the three applied projects are all encouraging specific extensions of adaptive dynamics theory. This setup will ensure that the methodological pluralism underlying the Program's activities remains as fruitful as it has been in the past. For example, research on evolutionary fisheries management requires integrating insights from adaptive dynamics theory with those from structured population dynamics. Research on speciation processes mandates the bridging between adaptive dynamics theory and approaches pioneered in population genetics theory. Research into the evolution of cooperation, nowadays often targeting the dynamics of spatially extended populations with localized interactions, promotes the development of methods for deriving and analyzing spatial invasion fitness, thereby extending one of the most fundamental concepts of adaptive dynamics theory. Last but not least, the adaptive dynamics of complex phenotypes, currently developed by the Program, is certain to find important applications in studies of the evolutionary dynamics underlying cooperation, responses to exploitation, and community structure.

Cross-fertilization is also expected between the three applied research projects. For example, politically realistic suggestions for the incorporation of evolutionary effects in current fisheries management will have to be informed by systematic considerations for counteracting the 'tragedy of the commons', a central theme in the theory of cooperation (Hardin 1968). Moreover, the models the Program plans to develop in order to study processes of adaptation and speciation on realistically heterogeneous resource landscapes also have potential for analyzing the evolution of cooperation in groups of individuals that differ in the amount, quality, or composition of resources they can draw on to sustain their potentially cooperative interactions. Also, scrutinizing the evolutionary responses of food webs will help to achieve the widely touted goal of strengthening the ecosystem approach to fisheries management (Garcia et al. 2003).

Project 1: Adaptive Dynamics Theory

As has been mentioned above, a fundamental difficulty challenges the understanding and prediction of evolutionary change in realistic ecological settings. On the one hand, closer linkages between ecological and evolutionary research invariably reveal the ubiquity of frequency-dependent selection pressures on almost all life-history traits of interest. Such frequency dependence occurs whenever selection pressures depend on the phenotypic composition of a population, which is the rule in natural systems. On the other hand, the bulk of life-history theory, including essentially all textbook treatments, is still based on simplified optimization approaches, which are applicable only if selection is frequency-independent. The necessity of resolving this mismatch drives the development of adaptive dynamics theory (Metz et al. 1992, 1996a; Dieckmann and Law 1996; Geritz et al. 1997, 1998; for forerunning and related work see also Rosenzweig 1978; Eshel 1983; Matsuda 1985; van Tienderen and de Jong 1986; Taylor 1989; Nowak and Sigmund 1989; Christiansen 1991; Brown and Pavlovic 1992; Vincent et al. 1993; Abrams et al. 1993; Eshel et al. 1997; Abrams 2001). Sacrificing genetic for ecological detail, adaptive dynamics models are derived for asexual,

mutation-limited evolution, and have been shown to yield results that are robust to the relaxation of these formal assumptions under a wide range of circumstances. Research on adaptive dynamics theory has established IIASA as a respected hub in the corresponding international scientific community.

Research on evolutionary dynamics will have to overcome traditional divides that have riddled the field. Several methodological extensions are needed to further facilitate practical applications. In pursuit of this agenda, the Program will address six methodological tasks:

- Task 1.1: Advance general insights into spatially structured evolutionary processes.
- Task 1.2: Develop and apply new techniques for simplifying spatial complexity.
- Task 1.3: Consolidate the adaptive dynamics theory of complex phenotypes.
- Task 1.4: Enhance tools for investigating evolution in sexual populations.
- Task 1.5: Extend traditional techniques of dynamic programming.
- Task 1.6: Derive finite-size corrections to refine Kimura's limit.
- Task 1.7: Develop the evolutionary counterpart of classical bifurcation theory.

Project 2: Evolutionary Fisheries Management

Commercial exploitation is altering the genetic composition of fish stocks around the world. This evolutionary dimension of fisheries has been overlooked or downplayed for decades, so that fisheries scientists and managers are just now awakening to the formidable risks posed by further unmanaged fisheries-induced evolution (e.g., ICES 2002). In a broadly based research effort, the Program has assembled empirical evidence that (i) fisheries-induced evolution in life-history traits, especially in characters determining maturation, has been with us for the past fifty years without having been recognized; (ii) fisheries-induced evolution is occurring much faster than was previously believed; and (iii) fisheries-induced evolution will be difficult and slow to reverse through managerial interventions (Heino et al. 2002a,b; Heino and Godø 2002; Kenchington and Heino 2002; Engelhard and Heino 2003, 2004; Grift et al. 2003; Heino 2003; Heino and Dieckmann 2003; Barot et al. 2004a,b, 2005; Dieckmann and Heino 2004; Olsen et al. 2004, 2005). These findings highlight serious economic and ecological implications for sustainable yield, stock stability, and recovery potential.

Over the next few years, the Program will work on documenting the worldwide extent of fisheries-induced evolution, and on aiding fisheries scientists and managers in coping with the resultant challenges for the sustainable exploitation of living marine resources. The specific tasks to be tackled are as follows:

- Task 2.1: Document the extent of fisheries-induced evolution in a broad suite of traits.
- Task 2.2: Enhance the geographic and taxonomic scope of case studies.
- Task 2.3: Integrate genetic information into analyses of fisheries-induced evolution.
- Task 2.4: Refine eco-genetic models of fisheries-induced evolution.
- Task 2.5: Establish integrative assessments of multi-trait fisheries-induced evolution.
- Task 2.6: Elucidate the mechanisms that link fisheries-induced evolution to decreased stock stability, yield, and recovery potential.
- Task 2.7: Establish criteria for assessing the evolutionary vulnerability of exploited stocks.
- Task 2.8: Identify fisheries regimes that are least prone to induce detrimental evolution.

Project 3: Evolution of Cooperation

Studies of cooperation are essential for understanding the formation of societies and, more generally, the rallying of independent units around a common agenda (Camerer 2003). Such cooperation of selective units to form a higher-order unit is a central theme in the study of the major transitions in evolution (Maynard Smith and Szathmary 1997), and thus offers a common thread for studying diverse adaptive processes in biological and cultural evolution. Accordingly, studies of cooperation provide a bridge between biological and sociological perspectives on evolution. Such studies also include classical examples of frequency-dependent selection: the success or failure of cooperative strategies will always depend on the strategies followed by partners and opponents, and thus on the composition and structure of the evolving population (for reviews see Hofbauer and Sigmund 2003; Nowak and Sigmund 2004).

IIASA has a long and renowned tradition of using tools from systems analysis for investigating conditions facilitating the evolution of cooperation. The resulting theories are currently enjoying great attention thanks to a new wave of research in experimental economics that uses them as null models. The new approach challenges the rationality assumption underlying much of classical game theory. Recent research advances at IIASA have shed new light on the role of reputation for the evolution of indirect reciprocity (e.g., Brandt and Sigmund 2004, 2005), the importance of voluntary participation for sustaining high levels of cooperation (e.g., Hauert et al. 2002; Sigmund et al. 2004), the joint evolutionary dynamics of cooperation and mobility (Le Galliard et al 2003, 2005), and on the effect of rewards and punishment in public goods games (e.g., Sigmund et al. 2001; Brandt et al. 2003). This last line of research also illustrates how recent evolutionary game theory is pushing beyond the traditional confines of pairwise interactions between players: in public goods games, individuals within a sizeable group have to decide whether they will contribute towards a group-level goal or take a free ride on the effort of others.

The following is a list of problems the Program plans to address:

- Task 3.1: Investigate 'win-stay, lose-shift' strategies in spatial games of direct reciprocation.

- Task 3.2: Investigate the effects of temporal and spatial heterogeneity on direct reciprocation.

- Task 3.3: Devise and analyze alternative action and assessment modules for indirect reciprocation.

- Task 3.4: Systematically examine the effects of errors on the evolution of indirect reciprocation.

- Task 3.5: Compare alternative deterministic approximations of game dynamics.

Project 4: Evolving Biodiversity

The evolutionary dynamics of biodiversity address some of the most fundamental questions of all biological research. Such understanding needs to be advanced at three levels. First are new insights into the evolutionary dynamics of single species. Processes of adaptive speciation, which result from directional selection towards a persistent regime of frequency-dependent disruptive selection, contribute to the formation of biodiversity (for reviews see Dieckmann et al. 2004). On the other hand, processes of evolutionary suicide cause the selection-driven extinction of species (Matsuda and Abrams 1994; Ferrière 2000; Gyllenberg et al. 2002; Parvinen 2004). At a second level, coevolutionary dynamics mold pairwise ecological interactions within small sets of species. Such studies focus on evolving predator-prey interactions, mutualisms, symbiotic structures, competitive interactions, and omnivory (e.g., Marrow et al.

1996; Law et al. 1997; Law and Dieckmann 1998; Kisdi 1999; Doebeli and Dieckmann 2000; Dercole et al. 2002; Dercole and Rinaldi 2002; Dercole 2003; HilleRisLambers and Dieckmann 2003; Bronstein et al. 2004). Thirdly, the evolution and self-assembly of whole ecosystems is attracting mounting attention (for a review see Drossel and McKane 2003): first results from this burgeoning field demonstrate that the impacts of evolution on ecosystem composition and stability are profound.

In future, the Program will deepen insights into the evolutionary dimensions of biodiversity science by pursuit of the following tasks:

- Task 4.1: Establish and analyze integrative speciation models.

- Task 4.2: Investigate the effects of realistically fluctuating landscape patterns on adaptive speciation processes.

- Task 4.3: Analyze genetic evolution during adaptive speciation processes.

- Task 4.4: Investigate the relationship between evolution and chaotic dynamics.

- Task 4.5: Explore the evolution of biological control.

- Task 4.6: Explore new models of disease evolution and management.

- Task 4.7: Develop more realistic models of adaptive ecosystem evolution.

- Task 4.8: Extend work on the evolutionary consequences of harvesting to the ecosystem level.

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