# A General Review of Zoological Trends During the 20th Century

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## Abstract

Enormous progress has been made in zoology during the 20th century, largely due to a multitude of clever new technological advances: electron microscopes, oscilloscopes, radioisotopes, radiotelemetry, digital and satellite imagery, PCR and DNA sequencing, global positioning systems (GPS), rapid and affordable travel, unimaginable computing prowess, faxes and email. All this new technology has allowed zoologists to study things previously impossible. The century began with the rediscovery of Mendelian genetics, followed by the discovery of DNA structure, the genetic code itself, instinct and animal behavior, speciation, hybrids, parthenoforms, a new previously unknown Kingdom of chemosynthetic organisms, restriction enzymes, cloning, genetic engineering, genetic control of development, and understanding of metabolic pathways.

One of the strongest recurrent themes in biology this century has been to consider all sorts of phenomena within the context of natural selection. Phylogenetic systematics has revitalized many areas of biology, forcing and facilitating an evolutionary approach. Evolution provides the conceptual backbone of zoology. Zoologists study phenomena that range across vastly different spatial and temporal scales, from molecules to cells to organisms to populations to communities and entire ecosystems.

Like other scientists, most zoologists have rushed to embrace the reductionistic approach. Too often, workers at different levels look somewhat askance at the next higher level of approach. The reason for this hesitancy to accept the next higher level may be that one must slur over interesting detail at one's own level in order to practice biology at the next level up. Each level of approach offers distinct advantages but suffers from its own problems. Molecular biologists cannot "see" the objects of their studies, but they can do experiments in Eppendorf tubes in small spaces in a matter of hours. An experiment is planned before lunch, executed that afternoon and results are analyzed that evening or the next day. Rapid progress can be made with such a compressed timetable. Other sorts of biology require more space and greater patience. Funding for zoological research is strongly skewed towards molecular biology. We should all attempt to couple our approach to higher levels and we should be more tolerant of others working at higher levels of approach.

Funding should be spread more equitably across disciplines. We have made impressive strides in understanding phenomena at most levels of approach in biology, but the approach at the community-ecosystem level lags far behind others. Much more thought needs to be devoted towards attempts to connect community properties with those of individuals in populations. Examples of how community-level properties could emerge from attributes of individuals are given.

## Introduction

First, I'd like to thank the organizing committee for inviting me to present this opening address to the 18th International Congress of Zoology. I suspect that my Greek friends Petros Lymberakis, Moysis Mylonas, and Efstratios Valakos, were instrumental in my being chosen and I'd like to thank them as well.

I did not choose this title — it was "assigned" to me by the organizers.

How could anyone review a subject as broad as zoology over an entire century? It's the kind of challenging thing one would expect somebody like Ernst Mayr to do. I guess if you live long enough, you get a chance at something like this. Obviously, I won't be able to mention many things zoologists have discovered during the past one hundred years. Please, do forgive me if I fail to mention your own favorite area of research!

I've been a zoologist for only 35 to 40 years and I've seen rather massive changes and new developments during just these four decades. For example, when I entered graduate school in 1960, numerical taxonomy was just being invented. It quickly replaced "old fashioned classical systematics," and then, just as quickly, phenetics was swept away by phylogenetics, which has endured and become entrenched during the last several decades.

## Zoology has become Obsolete

I fear that I must begin with some bad news for all zoologists.

Zoology is rapidly becoming obsolete! Let me illustrate this with the example of my own ill-fated department at the University of Texas. It seems as if people get restless towards the end of centuries and they like to reorganize things to become more "modern." From 1892 to 1899, the University of Texas had a "School of Biology" which included botanists, geologists, and zoologists. As the end of the century drew near, in 1899, the University reorganized and created three new "departments" of botany, geology, and zoology. These departments thrived and became recognized as among the best in the world. But last year, in 1999, the powers that be at my University got restless and decided to reorganize biology once again. [After all, it was the end of another century!] The once proud Department of Zoology where I spent the last 32 productive years was abolished on the eve of its 100th birthday! Our Departments of Botany and Microbiology were also eliminated. We went back a century to the old 1899 plan and created a new "School of Biological Sciences." Departments were out now, replaced with four "Sections." Their major motivation must have been to emphasize molecular biology since two of the four new sections are:

**Molecular Cell and Developmental Biology**
and **Molecular Genetics and Microbiology**

Another strangely narrow small section is **Neurobiology.**

All three of these sections adopt a reductionistic approach.

In the fourth section, mine, we embrace an explicit anti-reductionistic approach. We call it

**Integrative Biology**

Our group includes botanists and zoologists who work on ecology, evolution and organismal biology. We understand the need to integrate across levels of organization and taxonomic groups. We engage in interdisciplinary research (for example, I'm an ecologist and I have a small DNA laboratory). We hope that zoological research will flourish in our section.

These four sections are expected to serve as focal points for research, but all activities including faculty hiring and promotion, undergraduate and graduate programs, teaching and advising, are now coordinated through the overarching School of Biological Sciences, which has its own Director and staff. The School is a sort of "super" department for the biological sciences.

What do you suppose they'll do when 2099 rolls around?? If, indeed, humans haven't gone extinct by then!

## Techniques and Technological Breakthroughs

When you think about the past century, the first things that pop into mind are new techniques and technological breakthroughs. Electron micrographs allow us to see and study phenomena at a microscopic level. Satellite imagery has given us "macrographs" that allow us to see and study very large phenomena like El Niño. Satellite imagery has been available long enough now (since 1972) that chronosequences can be used to follow cyclical phenomena such as fire succession in grasslands.

Oscilloscopes are a relatively old invention that greatly enhanced the ability of physiologists to study neural phenomena. Isotopes allow us to follow the movements of molecules through an organism or an ecosystem and to follow a given cell or cell lineage through development as well as many other things like carbon 14 dating.

Modern molecular biotechnological tools, such as restriction enzymes and gene splicing, now enable geneticists to transfer particular genes from one organism to another using vectors such as plasmids and various viruses. Human insulin and growth hormone are now routinely produced in chemostats of *E. coli* bacteria that have had human genes spliced into their genomes. Transgenic cows produce milk containing medically useful proteins such as human blood clotting factors (useful for hemophiliacs!) Genetically altered transgenic bacteria have been used as living vaccines that confer resistance to particular diseases such as typhoid. Such recombinant DNA technology has also enabled us to produce useful new life forms such as pollutant-eating bacteria that can help us to clean up what's left of our environment. Pest resistance and nitrogen-fixing genes are being spliced into crop plants with the hope of vastly increasing yields. Any day now, some enterprising genetic engineer will transplant elephant growth genes into cattle to make bigger and better cows! You want a bigger chicken: I'll transplant some ostrich genes into chickens! We are audaciously bypassing natural selection and creating whatever phenotypes we think best.

A large percentage of US crops (corn, soybeans, cotton, tomatoes, etc) are genetically engineered and are now being grown commercially. More transgenic organisms will eventually be designed for release into nature. Genetically engineered organisms could have adverse effects on other species in natural ecosystems. We already have enough natural pests and certainly don't want to make any new ones! Unfortunately, we still know far too little to engineer ecological systems intelligently. Obviously genetic engineers should work hand in hand with ecological engineers (a nearly non-existent breed)!

Radiotelemetry has advanced to the point that very small transmitters can be attached to small animals and used to follow their movements.

Large animals like sea turtles and whales now carry devices that transmit their locations to satellites which download the data at prescribed times and positions. You can now be anywhere and follow a whale's migration from the arctic to the Antarctic.

In many ways, this is the best time ever to be a zoologist. We have easy access to anywhere in the world via rapid and affordable travel. We can go almost anywhere anytime and there are still bits and pieces of wilderness left scattered around the globe. Global positioning systems (GPS), invented for military purposes, now allow us to get relatively exact co-ordinates for any spot on earth quickly and with ease. Modern biological technological tools such as the polymerase chain reaction (PCR) allow us to amplify tiny amounts of DNA, which can now be sequenced relatively easily and inexpensively. DNA sequences can be used to establish degrees of relatedness among animals and to recover robust phylogenies, which can be used to infer probable evolutionary pathways.

I have been using computers and the Internet ever since their inception. I learned FORTRAN in grad school during the early 1960's and I wrote my own programs to do statistical analyses on one of the first vacuum tube IBMs (it took up a entire large room and could not even match one of today's low-end desktop personal computers). The speed with which personal computers have been improved is awesome. Just a few years ago, I treasured floppy disks. Now I almost never use them, only 100 meg zip disks. When my hard drive failed, I upgraded from 4 gigs to 38 gigs for only $289. Recently we got a 400 megahertz G4 which processes 128 byte bits rather than 32 byte bits. Being twice as fast and processing 4 times as much information at each step makes this computer eight times faster than last year's. Such computing prowess was unimaginable a mere decade ago. People reading this 10 years from now will undoubtedly laugh at how modest my fancy new computer was!

Today you can collaborate with people around the world with ease using faxes and email. While your colleague on the other side of earth is sleeping, you work, emailing it to him at the end of your day. Then, he or she plugs away at it while you sleep. Together, you can work around the clock!

## Major Developments

Now let's consider some other major developments in zoology during the last century. Of course, the century began with the rediscovery of Mendelian genetics and genetics has been a focal point all though the 1900's. Herman Mueller discovered that x-rays cause mutations. Mid century came the discovery of the structure of DNA, then the genetic code itself, the machinery of genetics, transcription, translation, etc. Instinct and animal behavior came to the fore, as did speciation, hybridization and parthenogenesis. The late W. D. Hamilton (and others) developed the idea of kin selection and inclusive fitness. Studies of sexual selection abounded (Andersson 1994). A new kingdom of chemosynthetic organisms was discovered. Metabolic processes such as the Kreb's cycle were understood for the first time. These still need to be placed in an evolutionary perspective ... how do metabolic pathways evolve? Why are they sometimes dismantled? The vast majority of mammals can synthesize ascorbic acid but humans cannot and must supplement their diets with Vitamin C. Many aspects of the genetic control of development, including developmental plasticity and canalization, have been elucidated, but much more remains to be learned. Phylogenetic systematics has revitalized many areas of biology and has both forced and facilitated an evolutionary approach.

## Evolution is Our Conceptual Backbone

One of the strongest recurrent themes in biology this century has been to consider all sorts of phenomena within the context of Darwinian natural selection. Dobzhansky (1971) said that "nothing in biology makes sense except in the light of evolution."

Evolution provides the conceptual backbone of all zoology.

## Natural Selection: the ultimate inventor

Natural selection is surely the ultimate inventor: a short list of some of its many patents includes flight, fusiform shapes, celestial navigation, echolocation, insulation, infrared sensors, hypodermic needles, plus a wide variety of pharmeceuticals including analgesics, antibiotics, diuretics, emetics, laxatives, and tranquilizers.

As another example of natural selection, consider gecko feet. These lizards can run up a pane of glass and even run upside down across a ceiling. Scanning electron micrographs show literally ***millions*** of elaborate very fine hairlike setae, each bearing tiny hooks and ***hundreds*** of spatulae which allow these lizards to gain purchase on almost any surface including very smooth ones (Hiller 1976). A single individual gecko can have as many as a ***billion*** spatulae! Several mechanisms of adhesion have been proposed, including suction, glue, electrostatic attraction, and friction. Gecko feet still stick in a vacuum, eliminating suction. Gecko feet have no glands, making glue most unlikely. Experiments using x-rays to ionize air have eliminated the possibility of electrostatic attraction. A smooth pane of glass offers very little in the way of friction, although friction would certainly be quite important when climbing on any rough surface.

In a very interesting recent study published in *Nature* (Autumn *et al.* 2000) of gecko setae, scientists removed a single seta from a large Tokay gecko and under a microscope glued it with epoxy to an extremely fine wire. Each seta ends in hundreds of spatulae, which press up and conform to the substrate. Direct forces of setal attachment were measured with an extremely tiny (about 100 x 100 micrometers) high-tech micro-electromechanical sensor (a two dimensional "dual-axis piezoresistive cantilever fabricated on a single-crystalline silicon wafer"). Earlier work that had rejected two previously proposed mechanisms of adhesion, suction and friction (Hiller 1968), had demonstrated that intermolecular forces, or van der Waal's forces, provided the adhesion. Van der Waals forces are basically like gravitational forces, but acting between molecules. Autumn et al's amazing high-tech study provided indirect support for such intermolecular forces. Van der Waal's forces require exceedingly intimate contact between a gecko's spatulae and the surface and they are extremely weak at distances greater than atomic distance gaps. These authors estimate that if a gecko's entire billion spatulae were simultaneously engaged with substrate molecules, the force holding a gecko to the substrate would be over 500 pounds per square inch!

With such powerful forces, one might expect geckos to be plastered against their substrates unable to move. During a powerful cyclone on Mauritius (Vinson & Vinson 1969), *Phelsuma* day geckos were actually beaten to death by the furious flapping of leaves they were on — but these dead geckos nevertheless remained firmly attached to the leaves! How do geckos manage to break such strong bonds? How do they control their powerful feet and toes? Autumn *et al.* (2000) liken the complex behavior of toe uncurling during attachment to blowing up an inflating party favor, whereas toe peeling during detachment is analogous to removing a piece of tape from a surface. During running, geckos peel the tips of their toes away from a smooth surface. Toe peeling may have two effects. First, it could put an individual seta in an orientation or at a critical angle that aids in its release. Second, toe peeling concentrates the detachment force on only a small subset of all attached setae at any instant (Autumn *et al.* 2000). Indeed, one of the great remaining mysteries is why don't such clinging toe pads pick up all sorts of debris?

These authors comment that manufacture of such small, closely packed arrays mimicking gecko setae is currently beyond the limits of human technology. Nevertheless, the natural technology of gecko foot-hairs could provide biological inspiration for future design of remarkably effective re-usable dry adhesives. Perhaps one day, people wearing gecko skin gloves will climb cliffs and buildings! If so, natural selection will hold the patent!

## Biological Hierarchies: Time and Space Scales

Zoology has a complex hierarchical organization. Zoologists study phenomena that range across vastly different spatial and temporal scales, from molecules to cells to organisms to populations to communities and entire ecosystems (Fig. 1). Across this broad range of scale, factors vary by many orders of magnitude. Emergent properties arise at each level. For example, glycolysis is a property shared by some metabolic pathways but it is not a property of a molecule. Dominance or recessiveness are properties

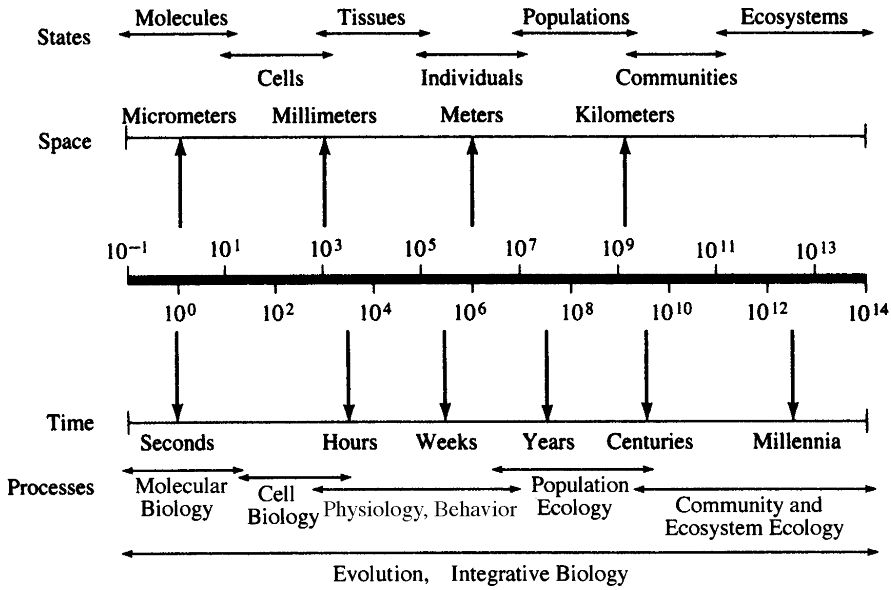


**Fig. 1.** Diagrammatic representation of the time-space scaling of various biological phenomena. Community and ecosystem phenomena occur over longer time spans and more vast areas than suborganismal- and organismal-level processes and entities. Most subdisciplines of biology take a narrow reductionistic approach. A broader integrative approach across all these levels of organization must be adopted.

shared by some genes but not of nucleotides. Sexual behavior is a property shared by some organisms but not of a gene. Sex ratio and population density are properties of groups of organisms but not of single animals. Food web connectance is a property of a community but not a property of a population.

Dan Brooks (1988) gave a nice example: (1) individuals move and disperse during their lifetimes, (2) over the lifetimes of multiple individuals, immigration and emigration take place between and among populations, giving rise to metapopulation structure, (3) over still longer time and space scales, geographical ranges shift in response to changing climates and geotectonic movements, ultimately leading to geographical patterns of diversity.

Molecular biology is small and fast. You can do multiple experiments in a few rooms using tiny Eppendorf tubes. In some cases, a researcher can plan an experiment while driving to work, execute the experiment early in the AM, go to lunch, and analyze the results later that afternoon. The next day a paper can be written and submitted to *Nature.* Simple causality reigns in molecules.

In contrast, community ecology requires lots of space and time. It may take decades to acquire results. Community ecology is not for the impatient or feint of heart. Multiple causality is the rule and constitutes an effective roadblock.

People are impatient — they want results, recognition and fame NOW, not later.

Many scientists adopt a reductionistic approach: take something apart into its component pieces and then try to put it back together again. The molecules are in motion, but knowing their positions and paths, can you extrapolate to explain phenomena at higher levels? An alternative integrative approach attempts to understand an entire complex entity across levels of organization, although some scientists express disdain for such a perspective. Both the reductionistic and integrative approaches can offer insights, often of very different sorts, into how a biological entity operates.

As we race to embrace molecular biology, many have been neglecting higher levels of approach. Indeed, it is worse than simple benign neglect. People working at each level actually express disdain for those struggling to work at higher levels. Molecular biologists think cell biology is sloppy because it necessarily slurs over interesting detail. Cell biologists find physiology crude. Organismal biologists wonder how population biologists can gloss over so much important biology of organisms. Population biologists scoff at community ecologists. Such narrow-minded snobbery towards higher levels of approach is inadvisable and unacceptable. It has resulted in funding being diverted more and more towards molecular biology and away from other disciplines like ecology.

Worse, traditional areas of zoology like comparative anatomy and physiology are no longer deemed important and therefore are not attracting new graduate students. "Ology" courses, such as protozoology, entomology, ichthyology, herpetology, etc. have disappeared from curricula everywhere. When everyone has become a molecular biologist, who is going to be able to tell molecular biologists what they are studying. Who will describe new species? Understanding molecular interactions seldom provides great insights into evolutionary forces molding adaptations.

This is perilous because all levels of approach are necessary to truly understand any biological phenomenon. We need to integrate from molecules to communities.

## Proximate versus Ultimate Factors

Consider the question "Why do migratory birds fly south in the autumn?" A physiologist tells us that a bird compares photoperiod against its internal biological clock. Decreasing day length stimulates hormonal changes, which in turn alter bird behavior with an increase in restlessness. Eventually this "Wanderlust" gets the upper hand and the birds head south. In contrast, an evolutionist would most likely explain that, by virtue of reduced winter mortality, those birds that flew south lived longer and therefore left more offspring than their non-migratory ancestors. Over a long period of time, natural selection resulted in intricate patterns of migratory behavior, including the evolution of celestial navigation, by means of differential reproductive success.

The physiologist's answer concerns the mechanism by which avian migratory behavior is influenced by immediate environmental factors, whereas the evolutionist's response is couched in terms of what might be called the strategy by which individual birds have left the most offspring in response to long-term consistent patterns of environmental change (i.e., spring bloom, high winter mortality). The difference between them is in outlook, between thinking in an "ecological" time scale (now time) or in an "evolutionary" time scale (geological time). At the physiologist's level of approach to science the first answer is complete, as is the evolutionist's answer at her or his own level. Ernst Mayr (1961) termed these the "how?" and "why?" approaches to biology.

They have also been called the "functional" and "evolutionary" explanations and the "proximate" and "ultimate" factors influencing an event (Baker 1938).

The first involves short-term cues whereas the second is a long-term strategy for passing on genes. Neither is more correct; a really thorough answer to any question must include both, although often only the first can be examined by direct experiment. Nor are those two ways of looking at biological phenomena mutually exclusive; behavioral, physiological and ecological events can always be profitably considered from within an evolutionary framework and vice versa. To understand avian migration, one needs to know about both immediate mechanisms and evolutionary forces.

We should all attempt to couple our approach to higher levels and we should be more tolerant of others working at higher levels of approach. Funding needs to be spread more evenly across all levels of approach rather than most of it being devoted to molecular biology.

## Community Ecology

Community structure concerns all the various ways in which members of communities relate to and interact with one another, as well as any community-level properties that emerge from these interactions. Just as populations have properties that transcend those of the individuals comprising them, communities have both structure and properties that are not possessed by their component populations. You can think of a community as a complex network of interacting populations.

Ecologists are not very interested in captive animals. Their subjects are wild organisms in natural settings, with a normal environment in which that particular creature has evolved and to which it has become adapted. Rolston (1985) made a useful analogy: he likened life on earth to a book written in a language that humans can barely read. Each page in this book of life represents a species, describing not only its phylogenetic relationships, but also its interactions with its physical and biotic environments, as well as its relationships with its competitors, parasites, predators, and prey. Each chapter represents a biome with pages describing all of its component species. Zoologists are just now acquiring the skills necessary to read and decipher this book, but the poor book is tattered and torn, pages are missing (extinct species such as passenger pigeons), and entire chapters have been ripped out (e.g., the tall grass prairies of midwestern North America). There is considerable urgency to study wild organisms in pristine natural habitats now. We must save as much of this vanishing book of life as possible. We must also read it before it is gone forever.

Community ecology has to attract population ecologists who are well versed in natural selection. It has become the province of systems ecologists and ecosystem engineers: more born-again population ecologists should become community ecologists. Community ecology is doubtlessly one of the most difficult kinds of biology, but it has obvious utility as we approach oversaturation of this planet. Moreover, data must be gathered now because so many systems are vanishing. Community ecology is also very promising. Major new discoveries, potentially things as important as DNA and natural selection, remain undiscovered because biologists have shied away from this discipline.

Community ecologists are still in the process of developing their vocabulary. Identification of appropriate aggregate variables or macrodescriptors (Orians 1980) is essential, but constitutes a double-edged sword; macrodescriptors allow progress but simultaneously constrain the directions that can be pursued. To be most useful, macrodescriptors must simplify population-level processes while retaining their essence without fatal oversimplification. Examples include trophic structure, connectance, rates of energy fixation and flow, ecological efficiency, diversity, stability, distributions of relative importance among species, guild structure, successional stages, and so on. At this early stage in community ecology, we should not become overly locked in by words and concepts until we are confident that we are going in the most fruitful directions. Moreover, a diversity of approaches seems desirable. Even the trophic level concept should not be inviolate.

A major pitfall for community ecologists is that communities are not designed directly by natural selection (as are individual organisms). We must keep clearly in mind that natural selection operates by differential reproductive success of individual organisms. It is tempting, but dangerously misleading, to view ecosystems as "superorganisms" that have been "designed" for efficient and orderly function. Antagonistic and asymmetric interactions at the level of individuals and populations (such as competition, predation, parasitism and even mutualisms) must frequently impair certain aspects of ecosystem performance while enhancing other properties.

Much more thought needs to be devoted towards attempts to connect community properties with those of individuals in populations (Pianka 1992). Terrestrial succession offers a possible example of how community-level properties could emerge from those of individuals. For an individual plant, a fast rate of photosynthesis and hence a rapid growth rate and high rate of reproduction are presumably incompatible with shade tolerance, and hence competitive ability in a light-limited situation. In contrast, shade tolerance and an ability to compete require slower rates of photosynthesis, growth and reproduction as well as relatively larger offspring. Such physiological trade-offs at the level of individuals could very well dictate many of the sequential patterns of species replacement (i.e., colonizing species to climax species) that characterize terrestrial succession.

Another example concerns ecological energetics. Only about 10% to 15% of the energy at any given trophic level is available to the next higher trophic level (an "ecological efficiency" of 0.10 to 0.15). This low efficiency has become a sort of rule for how natural communities behave. Genetic engineers tinkering with plant genes hope to increase ecological efficiency by making transgenic crop plants.

Why are natural communities so inefficient? Natural selection operating on individual predators favors more efficient predators — this in turn increases efficiency of flow of energy up through the trophic levels but reduces a system's stability. In homogeneous simple predator-prey systems, efficient predators harvest their prey to overexploitation, driving it extinct and then starving to death themselves. Selection operating on individual prey always favors escape ability, which reduces energy flow and enhances stability, exactly the reverse effects as those operating on predators. Heterogeneous complex habitats offer hiding places where prey can take refuge from predators, thus reducing energy flow and enhancing stability. In the coevolutionary arms' race between a predator and its prey, the prey must remain a step ahead of their predators, or they are overharvested to extinction. As a corollary, community-level properties of ecological efficiency and community stability may in fact be inversely related precisely because natural selection operates at the level of individual predators and prey. Thus, the apparent constancy and low level of ecological efficiency observed in natural ecosystems could be a result of the "compromise" that must be reached between coevolving prey and their predators. Humans seem to feel that we do not have to obey ecological rules — we think that we are somehow above nature. Soon we may find out that we are not!

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