

Biodiversity Studies: Science and Policy

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Biodiversity studies comprise the systematic examination of the full array of different kinds of organisms together with the technology by which the diversity can be maintained and used for the benefit of humanity. Current basic research at the species level focuses on the process of species formation, the standing levels of species numbers in various higher taxonomic categories, and the phenomena of hyperdiversity and extinction proneness. The major practical concern is the massive extinction rate now caused by human activity, which threatens losses in the esthetic quality of the world, in economic opportunity, and in vital ecosystem services.

FROM LINNAEUS TO DARWIN TO THE PRESENT ERA OF cladograms and molecular evolution, a central theme of biology has always been the diversity of life. A new urgency now impels the study of this subject for its own sake: just as the importance of all life forms for human welfare becomes most clear, the extinction of wild species and ecosystems is seen to be accelerating through human action (1). The dilemma has resulted in the rise of biodiversity studies: the systematic examination of the full array of organisms and the origin of this diversity, together with the methods by which diversity can be maintained and used for the benefit of humanity. Biodiversity studies thus combine elements of evolutionary biology and ecology with those of applied biology and public policy. They are based in organismic and evolutionary biology in the same manner that biomedical studies are based in molecular and cellular biology. They include the newly emergent discipline of conservation biology but are even more eclectic, subsuming pure systematic research and the practical applications of such research that accrue to medicine, forestry, and agriculture, as well as research on policies that maximize the preservation and use of biodiversity. In biodiversity studies, the systematist meets the economist and political scientist. In this article we will present some of the key issues that newly link these two principal domains.

Species Formation

A rich medley of models has been constructed to account for the origin of species by reproductive isolation. Two broad categories have been substantiated by empirical evidence. The first is poly-

ploidy, the multiplication of entire chromosome numbers within individual species or within hybrids of species, a process that isolates the new breed from its ancestor in one step. This instantaneous mode has generated 40% of contemporaneous plant species and a much smaller number of animal species (2). Of comparable importance is geographic (or allopatric) speciation, the origin of intrinsic isolating mechanisms in two or more daughter populations while they are isolated by a geographic barrier, such as a sea strait, desert basin, or mountain range. Evidence of this two-step process, which occurs widely in plants and animals, has been documented minutely, often to the level of the gene, in birds, mammals, and a few groups of insects such as drosophilid flies and butterflies (3).

The diversification processes of polyploidy and geographic isolation are generally appreciated because they follow an easily traced pathway of measurable steps. Other modes of speciation are more difficult to conceive and test, but this does not mean they do not occur widely. Perhaps the most common is nonpolyploid sympatric speciation, in which new species emerge from the midst of parental species even when individuals of both populations are close enough to intermingle during part of their life cycles. The dominant process of this category, at least the one most persuasively modeled and documented, is by intermediate host races. Members of the parental species feed upon and mate in the vicinity of one kind of plant; they give rise to an alternate host race that shifts to a second species of host plant growing nearby; the two races, thus isolated by their microhabitat differences, diverge further in other traits that reinforce reproductive isolation. Sympatric speciation may play a key role in the origin of the vast numbers of insects and other invertebrates specialized on hosts or other types of microhabitats. The early stages are difficult to detect, however, and few studies have been initiated in the invertebrate groups most likely to display them (4).

Certain forms of speciation can thus occur very rapidly, within one to several generations. And when species meet, they can displace one another genetically within ten or fewer generations, reducing competition and the likelihood of hybridization (5). A question of central importance is the impact of high speciation rates on standing diversity. Although the probability of extinction of species within a particular group at a particular place (say, the anole lizards of Cuba) eventually rises with the number of species, the number of species should increase with greater speciation rates at all levels up to equilibrium. But does it really? And if so, in which groups and to what degree?

Current Levels of Biodiversity

Also in an early stage, and surprisingly so, is the elementary taxonomic description of the world biota. At the present time approximately 1.4 million species of plants, animals, and microorganisms have been given scientific names (1, 6). Terrestrial and freshwater species diversity is greater than marine diversity. The

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overwhelming elements are the flowering plants (220,000 species) and their coevolutionary partners, the insects (750,000 species). The reverse is the case at the highest taxonomic levels, with all of the 33 living animal phyla present in the sea and only 17, or half, present on land and in fresh water (7).

Known species diversity is only a small fraction of actual species diversity, especially in the invertebrates and microorganisms. In this century the class Insecta has always been considered the most speciose group at the class level. As early as 1952, Sabrosky estimated that the number of living species is as high as 10 million (8). In 1982, Erwin found that beetle diversity in Neotropical trees, revealed in samples knocked down by insecticidal fogs, suggest far higher levels of insect and other arthropod diversity in tropical rain forests than had previously been estimated for the entire world fauna and flora (9). His figure, 30 million, was reached by extrapolating from counts of beetle species (1200) in a Panamanian tree species through estimates of total arthropod diversity per tree species to the percentages of species limited to each tree species to the total of tree species in tropical rain forests. Stork (10) reassessed this bold extrapolation, and in essence agreed with it, adding data of his own from Indonesian forests to produce a possible range of 10 to 80 million tropical forest arthropods. The most sensitive parameter remains the degree to which species of beetles and other arthropods are found uniquely on individual tree species.

In fact, because the life of the planet remains mostly unexplored at the species and infraspecies levels, systematists do not know the species diversity of the total world fauna and flora to the nearest order of magnitude. It is easily possible that the true number of species is closer to 10^8 than 10^7 . Relatively little effort has been expended on nematodes, mites, or fungi, each highly diverse and containing undescribed species that could easily range into the hundreds of thousands or millions. Bacteria, with only about 4000 described species, remain a terra vitae incognita because of the astonishingly small amount of research devoted to their diversity, as opposed to the genetics and molecular biology of select species.

Hyperdiversity

Certain taxa are hyperdiverse, that is, they contain more species, genera, or higher ranked groups within them than expected by a null model of random assortment (11). Examples include arthropods among animal phyla, insects among arthropods, rodents among mammalian orders, orchids among monocotyledonous plant families, *Sciurus* among the genera of Sciuridae (squirrels), and so forth. It can be expected in a Darwinian world, where chance and opportunism prevail, that production of great diversity depends to substantial degree on special adaptations allowing penetration of multiple niches, such that each hyperdiverse group has its own magic key. For example, the ants appear to have expanded by virtue of fungistatic secretions, series-parallel work operations, and a highly altruistic worker caste (12). But recent research has also begun to identify properties possessed by many groups: small size, permitting fine niche subdivision (7, 13, 14); phytophagy and parasitism with specialization on hosts (15); specialized life stages that allow species to occupy multiple niches; entry into new geographic areas with subsequent adaptive radiation and preemption; and greater dispersal ability, promoting the colonization of empty areas. Southwood has neatly summarized the likely causes of the extreme hyperdiversity of insects as "size, metamorphism, and wings" (13).

Hyperdiversity also occurs in certain habitats and geographical areas. The strongest trend worldwide is the latitudinal diversity gradient, with group after group reaching its maximum richness in

the tropics and most particularly in the tropical rain forests and coral reefs. (Exceptions include conifers, salamanders, and aphids.) The hyperdiversity of continental rain forests is legendary. Gentry found about 300 tree species in single-hectare plots in Peru (16), to be compared with 700 native tree species in all of North America. A single tree in the same area yielded 43 species of ants in 26 genera, about equal to the ant fauna of the entire British isles (17). Explaining the latitudinal diversity gradient has proven an intractable problem. But clues exist which when pieced together suggest the possibility of a general explanation, involving climatic stability and extreme biological specialization and niche division (18).

Natural Extinction

One of the qualities reducing diversity in particular groups is extinction proneness, which renders populations vulnerable to environmental change and reduces taxonomic groups to one or a very few threatened species. A threatened or endangered species (the two grades commonly employed by conservationists) is one with a high probability of extinction during the next few years or decades. The principal demographic properties contributing to the status are a low maximum breeding population size and a high coefficient of variation in that size (19). When the breeding size drops to a hundred or less, the likelihood of extinction is enhanced still further by inbreeding depression (20).

The overall natural extinction rate (at times other than mass extinction episodes) estimated from fossil data to the nearest order of magnitude is 10^{-7} species per species year (21). This estimate refers to true extinction, from the origin of a species to the extinction of that species and any species descended from it (altogether, called the clade) and excludes "pseudoextinction," the evolution of one species into another. Wide variation exists among major taxonomic groups in the longevity of clades. Mesozoic ammonoid and Silurian graptolite clades lasted only 1 million to 2 million years, whereas most other Paleozoic and Mesozoic invertebrate clades lasted closer to 10 million years (21). In general, planktonic and sessile marine animals, including corals and brachiopods, have had higher extinction rates than mobile benthic animals such as gastropods and bivalves (22). Using anatomical evidence from fossils and comparisons with related living species, paleobiologists have begun to infer the determinants of clade longevity by relating the adaptations of the organisms to maximum population size, population fluctuation, and dispersal ability (23).

Human-Caused Extinction

Biodiversity reduction is accelerating today largely through the destruction of natural habitats (1). Because of the latitudinal diversity gradient, the greatest loss occurs in tropical moist forests (rain forests) and coral reefs. The rate of loss of rain forests, down to approximately 55% of their original cover, was in 1989 almost double that in 1979. Roughly 1.8% of the remaining forests are disappearing per year (24). By the most conservative estimate from island biogeographic data, 0.2 to 0.3% of all species in the forests are extinguished or doomed each year (25). If two million species are confined to the forests, surely also a very conservative estimate, then extinction due to tropical deforestation alone must be responsible for the loss of at least 4000 species annually.

But there may well be 20 million or more species in the forests, raising the loss tenfold. Also, many species are very local and subject to immediate extinction from the clearing of a single habitat isolate, such as a mountain ridge or woodland patch (26). The absolute

extinction rate thus may well be two to three orders of magnitude greater than the area-based estimates given above. If current rates of clearing are continued, one-quarter or more of the species of organisms on Earth could be eliminated within 50 years—and even that pessimistic estimate might be conservative (25). Moreover, for the first time in geological history, plants are being extinguished in large numbers (27).

Another data set illuminating the urgency of dealing with the extinction problem measures the human impact on global net primary productivity (NPP) (28); global NPP is roughly the total food supply of all animals and decomposers. Almost 40% of all NPP generated on land is now directly used, coopted, or forgone because of the activities of just one animal species—*Homo sapiens*.

Since the overwhelming majority (possibly more than 90%) of species now exists on land, the 40% human appropriation there alone shows why there is an extinction crisis. Furthermore, the human population is projected to double in the next half-century or so—to more than 10 billion people. Most ominous of all, the widely admired Brundtland Report speaks of a five- to tenfold increase in global economic activity needed during that period to meet the demands and aspirations of that exploding population (29). If anything remotely resembling that population-economic growth scenario is played out, with an acceleration of habitat destruction, most of the world's biodiversity seems destined to disappear.

Why Should We Care?

The loss of biodiversity should be of concern to everyone for three basic reasons (1, 30). The first is ethical and esthetic. Because *Homo sapiens* is the dominant species on Earth, we and many others think that people have an absolute moral responsibility to protect what are our only known living companions in the universe. Human responsibility in this respect is deep, beyond measure, beyond conventional science for the moment, but urgent nonetheless. The popularity of ecotourism, bird-watching, wildlife films, pet-keeping, and gardening attest that human beings gain great esthetic rewards from those companions (and generate substantial economic activity in the process).

The second reason is that humanity has already obtained enormous direct economic benefits from biodiversity in the form of foods, medicines, and industrial products, and has the potential for gaining many more. Wheat, rice, and corn (maize) were unimpressive wild grasses before they were “borrowed” from the library and developed by selective breeding into the productive crops that have become the feeding base of humanity. All other crops, as well as domestic animals, have their origins in the genetic library, as do many medicines and various industrial products, including a wide variety of timbers (1, 30). Throughout the world almost a quarter of all medical prescriptions are either for chemical compounds from plants or microorganisms, or for synthetic versions or derivatives of them (31). One plant compound, quinine, is still a mainstay of humanity's defense against its most important disease, malaria.

Biodiversity is a precious “genetic library” maintained by natural ecosystems. But the potential of the library to supply such benefits has barely been tapped. Only a tiny portion of plant species has been screened for possible value as providers of medicines (31), and although human beings have used about 7000 plant species for food, at least several times that number are reported to have edible parts (1).

The third reason, perhaps the most poorly evaluated to date, is the array of essential services provided by natural ecosystems, of which diverse species are the key working parts. Ecosystem services include maintenance of the gaseous composition of the atmosphere, pre-

venting changes in the mix of gases from being too rapid for the biota to adjust. In Earth's early history, photosynthesizing organisms in the seas gradually made Earth's atmosphere rich in oxygen. Until there was enough oxygen for an ozone shield to form, the land surface was bathed in ultraviolet-B radiation. Up to some 450 million years ago life was confined to the seas. Only with the protection of the ozone shield were plants, arthropods, and amphibians able to colonize the land.

Significant alteration of the atmosphere has signaled the arrival over the past few decades of *Homo sapiens* as a global force, one capable of destroying most of biodiversity. As a result of human activities (32), the ozone shield has thinned by as much as 5% over Europe and North America (33), and there is some evidence that the surface intensity of ultraviolet-B radiation has increased there (34). Each spring the shield is now reduced over the Antarctic by approximately 50%. The global impact of the human economy is even more evident in the prospect of climatic change in response to increasing concentrations of greenhouse gases (35).

The organisms in natural ecosystems influence the climate in ways other than the role they play in regulating atmospheric gases. The vast rain forests of Amazonia to a large degree create the moist conditions that are required for their own survival by recycling rainfall. But as the forest shrinks under human assault, many biologists speculate that there will be a critical threshold beyond which the remaining forest will no longer be able to maintain the climate necessary for its own persistence (36). Deforestation and the subsequent drying of the climate could have serious regional effects in Brazil outside of Amazonia, conceivably reducing rainfall in important agricultural areas to the south. There also appear to be regional effects on climate when semi-arid regions are desertified (37), but their extent remains unknown.

The generation and maintenance of soils is another crucial service supplied most efficiently by natural ecosystems. Soils are much more than fragmented rock; they are themselves complex ecosystems with a rich biota (38). The elements of biodiversity in soil ecosystems are crucial to their fertility—to their ability to support crops and forests.

Many green plants enter into intimate relationships with mycorrhizal fungi in the soil. The plants nourish the fungi, which in turn transfer essential nutrients into the roots of the plant. In some forests where trees appear to be the dominant organisms, the existence of the trees is dependent upon the functioning of these fungi. On farms, other microorganisms play similar critical roles in transferring nutrients to crops such as spring wheat.

Organisms are very much involved in the production of soils, which starts with the weathering of the underlying rock. Plant roots can fracture rocks and thus help generate particles that are a major physical component of soils; plants and animals also contribute CO₂ and organic acids that contribute to the weathering of parent rock. More importantly, many species of small organisms, especially bacteria, decompose organic matter (shed leaves, animal droppings, dead organisms, and so on), releasing carbon dioxide and water into the soil and leaving a residue of humus, or tiny organic particles. These are resistant to further decomposition, help maintain soil texture and retain water, and play a critical role in soil chemistry, permitting the retention of nutrients essential for plant growth.

Soil ecosystems themselves are the main providers on land of two more essential ecosystem services: disposal of wastes and cycling of nutrients. Decomposers break wastes down into nutrients that are essential to the growth of green plants. In some cases, the nutrients are taken up more or less directly by plants near where the decomposers did their work. In others, the products of decomposition circulate through vast biogeochemical cycles before being reincorporated into living plants.

Another critical service provided by natural ecosystems is the

control of the vast majority of species that can attack crops or domestic animals. Most of those potential pests are herbivorous insects, and the control is provided primarily by numerous species of predacious and parasitic insects that naturally feed upon them.

While natural ecosystems are providing crop plants with stable climates, water, soils, and nutrients, and protecting them from pests, they also often pollinate them. Although honeybees, essentially domesticated organisms, pollinate many crops, numerous other crops depend on the services of pollinators from natural ecosystems. One such crop is alfalfa, which is most efficiently pollinated in cooler areas by wild bees.

The biodiversity in natural ecosystems also supplies people with food directly—most notably with a critical portion of their dietary protein from fishes and other marine animals. This service is provided by oceanic ecosystems in conjunction with coastal wetland habitats that serve as crucial nurseries for marine life.

The ecosystem services in which biodiversity plays the critical role are provided on such a grand scale and in a manner so intricate that there is usually no real possibility of substituting for them, even in cases where scientists have the requisite knowledge. In fact, one could conclude that virtually all human attempts at large-scale inorganic substitution for ecosystem services are ultimately unsuccessful, whether it be introductions of synthetic pesticides for natural pest control, inorganic fertilizer for natural soil maintenance, chlorination for natural water purification, dams for flood and drought control, or air-conditioning of overheated environments. Generally, the substitutes require a large energy subsidy, thereby adding to humanity's general impact on the environment, and are not completely satisfactory in even the short run (39).

It is important to note that in supplying ecosystem services the species and genic diversity of natural systems is critical. One might assume that one grass or tree species can function as well as any other in helping control the hydrologic cycle in a watershed, or that one predator will be as good as another in controlling a potential pest. But, of course, organisms are generally highly adapted to specific physical and biotic environments—and organic substitutions, like inorganic ones, are likely to prove unsatisfactory.

In sum, much of biodiversity and the quality of ecosystem services generated by it will be lost if the epidemic of extinctions now under way is allowed to continue unabated.

Public Policy

Many steps can be taken to preserve biodiversity, if the political will is generated. Perhaps the first step, which would be seen as especially extreme by Americans, would be to cease "developing" any more relatively undisturbed land. Every new shopping center built in the California chaparral, every hectare of tropical forest cut and burned, every swamp converted into a rice paddy or shrimp farm means less biodiversity.

In rich countries, stopping the more destructive forms of "development" is relatively simple in principle. Age structures are such that population shrinkage in most rich nations could be achieved with little effort (a few are already in that desirable mode). When new facilities are needed, they should replace deteriorating old ones. Forestry should be placed on a sustainable basis with careful attention to the conservation of precious reserves of old growth. And much more scientific effort and public support should go into biodiversity studies, including the cataloging of the genetic library and national biological inventories (1, 31).

In poor nations, the task is both more urgent and vastly more difficult. It cannot be accomplished immediately, and will not be accomplished at all without massive assistance from the rich. For

instance, stopping the expansion of cropland and pasture into virgin areas cannot be accomplished unless birth rates can be dramatically lowered and the development of sustainable high-yield agricultural systems is backed by land reform and a sound agricultural infrastructure and economy. In many cases, new social and economic systems must be developed in which preservation of biodiversity and its sustainable exploitation go hand in hand. The social, political, economic, and scientific barriers to achieving the goal are so formidable that nothing less than the kind of commitments so recently invested in the Cold War could possibly suffice to accomplish it. And we are 45 years late in starting.

But ending direct human incursions into remaining relatively undisturbed habitats would be only a start. Simultaneously, global cooperative efforts to reduce anthropogenic impacts on ecosystems, such as those directed at a reduction of emissions of greenhouse gases and ozone-destroying compounds, must be greatly enhanced. They are much more likely to be successful if population growth can be halted and the cessation of forest destruction can be achieved.

Finally, because humanity already occupies so much of Earth's surface, substantial effort should be directed at making areas already used by people more hospitable to other organisms. Those efforts can range from the substitution of game ranching for cattle and sheep ranching in many areas to the substitution of native vegetation for European-style lawns in desert cities.

If there is to be any chance of abating the loss of biodiversity, action must be taken immediately. The essential tactics of conservation are being developed within conservation biology, as a subdiscipline of biodiversity studies. The indispensable strategy for saving our fellow living creatures and ourselves in the long run, is, as the evidence compellingly shows, to reduce the scale of human activities. The task of accomplishing this goal will involve a cooperative worldwide effort unprecedented in history. Unless humanity can move determinedly in that direction, all of the efforts now going into in situ conservation will eventually lead nowhere, and our descendants' future will be at risk.

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 40. This article is dedicated to some of the key individuals who have influenced our thinking on biodiversity: W. L. Brown, E. Mayr, C. D. Michener, and R. R. Sokal; and the late J. H. Camin, R. W. Holm, and R. H. MacArthur. For helpful comments on the manuscript we are indebted to G. C. Daily, J. M. Diamond, A. H. Ehrlich, T. Erwin, J. Harte, M. E. Harte, C. E. Holdren, J. P. Holdren, T. Lovejoy, J. P. Meyers, S. Conway Morris, D. M. Raup, P. H. Raven, and M. E. Soul  .

Research Article

Convergence of Ets- and Notch-Related Structural Motifs in a Heteromeric DNA Binding Complex

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Analysis of the heteromeric DNA binding protein GABP has revealed the interaction of two distinct peptide sequence motifs normally associated with proteins located in different cellular compartments. The α subunit of GABP contains an 85–amino acid segment related to the Ets family of DNA binding proteins. The ETS domain of GABP α facilitates weak binding to DNA and, together with an adjacent segment of 37 amino acids, mediates stable interaction with GABP β . The β subunit of GABP contains four imperfect repeats of a sequence present in several transmembrane proteins including the product of the *Notch* gene of *Drosophila melanogaster*. These amino-terminal repeats of GABP β mediate stable interaction with GABP α and, when complexed with GABP α , directly contact DNA. These observations provide evidence for a distinct biochemical role for the 33–amino acid repeats, and suggest that they may serve as a module for the generation of specific dimerization interfaces.

SINCE THE INITIAL RECOGNITION OF A COMMON PROTEIN sequence motif in the *SWI6* gene product of *Saccharomyces cerevisiae* and the *Notch* gene product of *Drosophila melanogaster* (1), similar sequences have been identified in different biologically interesting proteins. The motif, variously termed the *cdc10*/

SWI6 or ankyrin repeat, consists of a 33–amino acid sequence often present in tandem arrays. This motif has been observed in the products of the *Notch*, *lin-12*, and *glp-1* genes, putative transmembrane proteins of *Drosophila melanogaster* and *Caenorhabditis elegans* that transmit signals critical for specification of cell fate (2); the product of *fem-1*, a *Caenorhabditis elegans* gene that regulates sex determination (3); *cdc10*, *SWI4*, *SWI6*, yeast proteins involved in cell cycle control (1, 4); ankyrin, a multifunctional protein of the red blood cell cytoskeleton (5); the product of *bcl-3*, a human gene located near a translocation breakpoint associated with some leukemias (6); the 105-kD precursor to the active 50-kD subunit of NF κ B/KBF1 (7); and I κ B, a regulatory subunit of NF κ B that inhibits DNA binding and has been implicated in cytoplasmic sequestration (8). Despite the widespread occurrence of the 33–amino acid motif, its functional role has heretofore remained obscure.

Our interest in the 33–amino acid repeat arose from studies of GA binding protein (GABP), a multisubunit DNA binding protein purified from rat liver nuclei (9). GABP was originally identified as a factor that binds to a cis-regulatory element required for VP16-mediated activation of herpes simplex virus (HSV) immediate early genes (10). Biochemical and molecular biological experiments have shown that GABP is composed of two distinct polypeptides, both of which are required for avid interaction with DNA (9, 11). The amino acid sequence of the GABP α subunit exhibits similarity to the Ets family of nuclear proteins, whereas that of GABP β contains a tandem series of 33–amino acid, *cdc10*/*SWI6* repeats (11). We now demonstrate that it is these two distinct protein sequence motifs that form the heteromeric interface between GABP α and GABP β .

We view the 33–amino acid repeat as a versatile module for the

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