

# The Ecosystem Level of Organization

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An ecosystem, as Paul Weiss has pointed out (p. 31), is a "paradigm of the principle of interdependencies, partly prestructured, partly in free systems interaction, which make it possible for organisms to mesh harmoniously with their environment and with one another, both individually and in groups, so as to exist, persist and thrive." It reflects the dualistic concept of systems in which discrete units are "enmeshed in, and in interplay with, an organized reference system of unified field dynamics of the collective of which they are the members" (p. 38). The discrete units in ecosystems are individual organisms, and their interplay emerges in populations and communities as subsystems, as well as in the dynamics of the ecosystem as a whole. The concept of an ecosystem as one end of a spectrum of hierarchically organized systems of increasing complexity, from atoms upward, provides an indispensable tool for understanding how nature, including man, is structured and how it works. In the present article an endeavor is made to apply the concepts of systems to the ecosystem level of organization.

First of all, it is important to understand more clearly the meaning of ecosystem in the context of this discussion. The term can be used legitimately to refer to any level of organized system, from cells to biocommunities, when

the total environment is included with the network of units and their interactions. In other words, by including the environmental matrix in which the network is enmeshed as part of a system, one conceptualizes an ecosystem. This is a logical approach, since no living unit, or network of units, survives except in an environment, which is as much a part of the system as the integrated network of units and their interactions. This broad concept of an ecosystem underlies all discussions of the higher-order systems from the population upward.

It is necessary also to distinguish an ecosystem as the highest level of hierarchically organized systems to provide a concept and a term for discussions at this level. In common currency an ecosystem is thought of as the integration of the communities of living organisms and their total non-living environment in a geographical region of the earth at a particular point in time, and this is the concept referred to in the present discussion. An ecosystem has no particular size, and its boundaries may not be distinct when one translates the concept to observable reality in nature. The selection of an operational system for research or management depends more on convenience than on rigid definitions. One may speak of "major" ecosystems in various geographic regions of the earth—such as tundra, tropical rainforest, deciduous hardwood forest, coniferous forest, grasslands, marine estuaries, or deserts. These terms evoke the concept of ecosystems, despite the apparent inadequacy of the labels which focus on vegetation to the exclusion of animals. It must be borne in mind also, that a major ecosystem embraces many subecosystems as component parts of the larger whole in any given geographical region.

Conceptually, the irreducible units of the higher levels of biological organizations in the three-dimensional network are the individual living organisms. They form the nodal points of the network, and their interactions form the strands of the network. The network is enmeshed in, and

integrated with, the environmental matrix; and the whole forms a population, community, or ecosystem. Symbolically, the individual organisms may be considered the irreducible units for systems above the organismic level, in a manner comparable to subatomic particles at the elemental level, and one can envision a field-organism complementarity similar to that of the field-particle complementarity in physics. At the atomic level, only about 50 subatomic particles are involved in the formation of about 100 chemical elements, which in turn form only a few thousand naturally occurring simple molecules. Living organisms are based on about one-fourth of the elements, and a relatively small number of simple molecules are involved in the elaboration of macromolecules. At the ecosystem level some 5 to 10 million different species are involved, and within a single species most of the members are genetically different from all the others. Thus the complexity of the field-organism complementarity at the ecosystem level is incomparably greater than that of the field-particle complementarity at the atomic level, and when one integrates the human mind with an already incredibly complex nonhuman ecosystem, it becomes apparent that the contemporary world ecosystem is not only more complex than one thinks it is, but more complex than one can think. An approach through hierarchically organized systems, on the other hand, enables one to comprehend significantly a great deal about the structure and functioning of the total ecosystem and its subsystems.

As a specific illustration of the complexity of ecosystems, consider Oxford University's estate at Wytham Woods, where Charles S. Elton studied the animal communities intensively for more than a quarter of a century. Here a rich pattern of open fields, limestone outcroppings, woodland, springs, and marshes is set in riverine surroundings. The complexity of this pattern of ecosystems within an area of about two square miles can be appreciated from the diversity of animal life, which includes an estimated 5,000

species, about 3,800 of which have been identified. To the animals one must add numerous species of plants and microorganisms that are also essential components of the ecosystems at Wytham Woods. Each species is represented by populations varying from a few individuals, for some of the rarer plants and larger mammals, to billions, for some of the microbes. Thus, on an individual basis, the number of interacting component units of living organisms in the system's network is astronomical, and the interplay among the organisms in their environmental context staggers the imagination.

Out of an incredible scramble of interactions between individual organisms, patterns of structure and processes emerge as integral configurations of populations, communities, and ecosystems. To begin with, the individuals of the same species in a given area at a particular time constitute an intraspecific local population with emergent attributes that reflect the collective behavior of the individuals—including natality, mortality, intrinsic rate of natural increase, sex and age structure, social behavior, social organization, and self-regulating mechanisms of numerical control. To persist within the ecosystem the population must maintain homeostatic stability from year to year. At a given season of the year the average number of individuals per unit area, or density, is remarkably similar to that of the previous year in most species, irrespective of the vicissitudes of weather conditions, variations in factors causing mortality, and other vagaries in factors that affect the increase or decrease in numbers. Explosions in populations, as in locust outbreaks, sporadic marine algal blooms known as red tides, deer irruptions in developmental stages of vegetation change, or the current human population, are exceptional phenomena of populations associated with major perturbations to the ecosystem. Periodic fluctuations in some animals such as the lemming, snowshoe hare, and ruffed grouse may represent adaptations to ecosystems of

harsh climates at high latitudes, in which a wide amplitude in the steady-state system has survival value.

Numerical homeostasis can be achieved through a variety of physiological and behavioral processes. Natality in population of white-tailed deer can vary through the number of ova released, the number of live births, and the minimum age at first conception. Under favorable environmental conditions, particularly with regard to food supply, about half of the females become pregnant while they are fawns, and the average number of offspring is more than two per female, whereas under poor nutrition fawns rarely breed, and the average number of offspring is less than one per female. In populations of elk the flexibility in natality is more restricted, since females have only one young at a time, but natality increases under favorable conditions through breeding of 50% or more of the yearling females, which would otherwise delay breeding until the age of 2½ years. While nutrition undoubtedly plays a major role in the regulation of natality, other more subtle interactions may be important, such as the psychology of crowding or territorial behavior. In the Australian magpie territoriality has been shown to regulate natality, and a large floating population in less favorable habitat harbors a high percentage of nonbreeding females. Although supporting evidence is still extremely limited, social behavior appears to be one of the most important population-regulating mechanisms among many of the higher forms of animal life, particularly in birds and mammals, functioning through natality or mortality, or both. Changes in a population's pool of genetic variation, at periodic high density in some species of small mammals, may provide a mechanism for numerical regulation. Parasitism or predation may play the dominant role in the regulation of some insect populations. Whatever mechanisms are involved in homeostatic regulation of numbers, a population must adjust to the total ecosystem through the intrinsic interplay of its members and through

extrinsic interplay with its total environment, if it is to survive as a component of an ecosystem. These self-adjustments of the population emerge from the field dynamics of the system, as determined by the collective, seemingly "intelligent," behavior of the member organisms. Furthermore, numerical recovery from exceptionally low levels is a manifestation of the resilience of population systems in returning to the original form following nondestructive disturbances, and confirms the integrated systems behavior of populations. Thus it is logical to conceptualize populations as systems at a higher order, next to and above that of the organismic level.

The interplay between populations of closely related species determines a niche structure, or spectrum of ways of life, through which competition for life requirements is reduced or excluded within an ecosystem. Five congeneric species of insectivorous warblers, for example, are able to coexist and nest in the same spruce forest, by dividing up the resources of the ecosystem in such a way that each species is limited by a different factor—different resources, the same resources at different times, or the same resources at different places—through unique patterns of behavior. Two of these species of warblers depend upon periods of superabundant food, while the others depend upon differences in feeding positions and nesting dates to reduce competition, and the overall effect is that each species inhibits its own population more than it does the populations of the other species. Similarly, slight differences in food habits, utilizing different grasses, the same species at different seasons, or different portions of the same species of grass, enable a spectrum of 10 to 20 species of ungulates to coexist and efficiently utilize the savannas of eastern Africa.

Niche structure emerges from the interplay between populations of different but closely related species, and provides an insight as to some of the mechanisms underlying speciation, and the formation of communities of population

systems of two or more species, and ultimately of whole ecosystems. Communities form more complex higher-level systems above intraspecific populations, with emergent properties not found at the lower levels of organized systems. In terms of observable structure, the physiognomy of terrestrial vegetation provides an excellent example of integral configurations at the community level. The layering of community systems as canopy, understory, and ground communities, provides an intricate structure of food and cover for animals, which in turn determines the structure of animal communities. The rich diversity of woody plants, as many as 1,000 species, in a high tropical rainforest with an elaborate layering of communities, provides an enormous variety of habitats for animals and opportunities for an endless variety of niches, the outcome of which is an incredible diversity among animal species. Another example of observable structure at the community level of systems is the physiognomy of sedentary communities of marine animals, including the corals, sea anemones, sponges, sea whips, and sea fans, so vividly displayed on TV in recent years. These structural arrangements of plant and animal communities recur in nature, with sufficient integrity as to be identifiable and serve as a systems level that is subject to scientific inquiry.

Because of its observability, vegetation (an integration of plant communities) has lent itself well to investigation, both in terms of structure and processes at the community level, so much so that the designation of major ecosystems is based on the earth's vegetation. The ecosystem concept seems to have grown out of studies of vegetation, in recognition of animal communities as integral parts of a higher-order system. The interrelatedness of plants is so well defined in some communities that one school of thought, in Europe, evolved a phytosociological approach, in which societies of plant populations are considered equivalent to a species, a viewpoint that exaggerates community integration

as fixed linear interactions and interlocking braces. Free systems dynamics probably characterizes the formation of plant communities more than linear chain reactions, but not to the extent that each population of plant species is distributed entirely and completely independently of all other populations. It is impressive that plant communities do emerge, despite the variability of individual behavior of plants and populations of plants, and the process by which this occurs is comprehensible in terms of systems dynamics. An appreciation of the probabilistic nature of the interactions is more readily developed through a systems approach, providing for statistical concepts and models of communities, through which to expand knowledge beyond that which is directly observable as vegetation in the field.

The process of vegetation change, or succession, on areas of abandoned farmland, forest clear-cuts followed by fire, or grassland released from heavy grazing by livestock, reflects the interactions of populations of different species of plants. Although the pattern of change is a continuum, "stages" can be recognized in the developing vegetation—such as forbs and annual grasses, perennial grasses, shrubs, and one or more types of forest. The underlying mechanisms of vegetation changes are not yet clear. It is thought that one community succeeds another, as the ecosystem is rendered less suitable for the existing plant communities and more suitable for the succeeding community. Relays of waves of plant disseminules from the surrounding ecosystems have been considered the primary source of new species composition during the process of succession. Recent studies in the northeastern United States cast doubt on the efficacy of this process as the dominant one in vegetation change, in view of the stability of shrub communities, and even herbaceous communities, following herbicidal removal of tree species. Most of the vegetation change in these 25-year studies seemed to emanate from plant species initially on the site at the time of abandonment from farming prac-



tices, but not to the total exclusion of the relay process. What is most remarkable is the relatively high predictability of the patterns of change, despite the highly probabilistic nature of the underlying mechanisms and the variability in the interactions between individual plants, which can best be interpreted on the basis of field continua and integral guidances of dynamic systems.

The process of succession involves developmental communities of animals and microorganisms as well as vegetation, and it also involves changes in the physical and chemical components of the area in which it occurs. It involves the total ecosystem, and although vegetation can be conceptually isolated for convenience in studying and managing this system, the interplay of plants, communities, and vegetation with other components of the ecosystem is essential to an adequate understanding of the process of vegetation change.

Populations; communities of populations of different organisms; vegetation as an integrated system of plant communities; biocommunities of populations systems of plants and animals; and human societies, can be viewed as major subsystems of an ecosystem in a geographical region of the earth, emerging from the field dynamics established by the collective behavior of the component organisms. All systems, from the organismic level downward, are also essential to the functioning of the total ecosystem, and it may be necessary to move to the molecular level to understand the limitations of ecosystem processes, such as energy flow, or the cycling of nitrogen, phosphorus, or other nutrients, but the phenomena that are unique at the ecosystem level seem to take form primarily out of its subsystems from the population upward.

An ecosystem is an open system with regard to the flow of energy that sustains it. Light energy, reaching the earth from the sun as photons, is converted to chemical energy in simple organic compounds, through the hydrogenation of

carbon in the process of photosynthesis in green plants. About half of the potential energy, or gross productivity, is utilized in metabolic respiration by the food-producing plants, some is stored temporarily in the biomass of plants, and the net productivity flows into two types of food chains, one leading to herbivores and carnivores, and the other to organisms of decay. At each trophic level in the ecosystem's web of food chains some of the energy is stored in body tissues, temporarily, as biomass. Ultimately, all of the fixed energy is degraded and radiated into space as heat. A trophic structure emerges—from the interactions of the primary producers (almost exclusively chlorophyll-bearing plants), herbivorous primary consumers, carnivorous secondary and tertiary consumers, and decomposers such as fungi and bacteria—as food chains, food webs, pyramids of biomass or standing crop, and pyramids of numbers with a supporting base of numerically superior primary producers and a few top carnivores. The flow of energy through food webs, until all of the potential energy captured from the sun is degraded to heat, represents an ecosystem process that is unique for the system as a whole. The efficiency of the system is rather low, with only 0.1 to 0.3 percent of the solar radiation being fixed, and a transfer rate of 10 to 20 percent as the energy flows from one trophic level to another. In a developmental ecosystem, progressing toward a mature steady-state system, a portion of the net productivity is incorporated into the structure of the system as biomass, and into an elaboration of interactions among an increasing diversity of species components. In a mature ecosystem the net productivity approaches zero with no energy left over and no net annual storage. Such ecosystems reflect an evolutionary trend toward highly diversified, complex, homeostatically stable systems that make the most efficient use of the nonliving environmental matrix. This includes efficient mechanisms for recycling of the chemical elements that form the basis for living systems, including

carbon, hydrogen, oxygen, sulfur, phosphorus, and several others, in respect to which an ecosystem is a closed system, subject to limitations when certain elements are in short supply. It is the complexity, arising from the diversity of organisms and their interplay, that determines the steady-state stability of mature ecosystems.

The total world ecosystem, prior to the advent of man, can be envisioned as a unified system with regional subsystems all tending toward increasing complexity and steady-state conditions. These nonhuman ecosystems represented the outcome of more than 3 billion years of evolutionary history, during which time upwards of 1 billion different species of organisms are estimated to have evolved, over 99 percent of which have become extinct. The ecosystems evolved as well as the species components. Terrestrial ecosystems are relatively recent evolutionary developments, dating back to about 400 million years ago, when living organisms began invading terrestrial environments from marine ecosystems. The evolution of arborescent vegetation enormously increased the opportunities for new niches, the proliferation of new species, and the development of highly complex ecosystems with self-regulating cybernetic controls, that provided relatively stable steady-state systems over long periods of time. About 2½ million years ago the human species was brought into being by these mature ecosystems. The resilience of these systems, exhibited in their capacity to recover from disturbances or perturbations imposed by the man-system over the past 5,000 years, is a measure of the integrity of ecosystems as highly organized dynamic systems. Man's technological capacity to destroy the integrity of ecosystems through irreversible changes is a relatively recent innovation.

The human mind, through which the man-system has been able to transcend many of the biological constraints of other forms of life, has added a new dimension to the world ecosystem. The term "noosphere" has been suggested

as a new world envelope of the collective human mind, comparable in concept to the lithosphere (the nonliving solid earth), the atmosphere (the nonliving gaseous envelope), the hydrosphere (the nonliving aquatic aspect), and the biosphere (including all of the living organisms taken as a whole, exclusive of the nonliving environment). Together, these five spheres constitute the ecosphere, or total world ecosystem. The viewpoint of the earth in terms of its envelopes is useful in understanding the structure of the world ecosystem and major processes, such as the hydrologic cycle involved in biogeochemical recycling of materials in the closed system, and it helps to introduce the concept of the noosphere as a recent evolutionary development. It is the noosphere, functioning through modern technology, that now threatens the integrity of the world ecosystem. The current changes may be comparable in significance to the biological revolution of 2 billion years ago, when aerobic respiration evolved as a mechanism through which energy became available in quantities several orders of magnitude above that which was possible through primitive anaerobic fermentation processes, setting the stage for the evolution of higher, more complex living systems.

From an ecosystem viewpoint man has not transcended nature, and with all his unique humanistic attributes man can be viewed as a system in nature—as an integral part of the ecosystem that brought him into being. Population systems of man are so dominated by anthropocentric views, that the biological aspects of human behavior, the demographic behavior of his populations, ecosystem processes, and the evolution of the noosphere, are overshadowed by man's preoccupation with the arts, religion, political and social systems, and the economics of moving energy, materials, and consumer goods through the system. Man is capable of irreversibly altering the total world ecosystem by increasing the carbon dioxide content of the atmosphere, to a point where the greenhouse effect could warm the earth

sufficiently to melt the polar ice caps; by interrupting vital processes such as photosynthesis, bacterial hydrogenation of sulphur, or nitrogen fixation by introducing new man-made chemicals, such as DDT and other highly toxic substances, into the ecosystem; by simplifying the species diversity and complexity of ecosystems, thereby destroying the resilience of systems to recover from disturbances; by reducing solar radiation by atmospheric pollution; and by increasing radioactivity to levels that are intolerable to living organisms.

The impact of man on the total ecosystem can be viewed as ecosystem processes at a new and higher-order level of systems organization, which can be conceptualized as the human ecosystem or the human-society-plus-total-environment level of organization. As a systems phenomenon the current biological revolution in the world ecosystem, brought on by the noosphere, can be viewed as being in a positive feedback phase, in which ever-higher levels of population encourage economic and technological growth at an ever-increasing expense to the diversity, complexity, and stability of the whole world ecosystem. If the real benefits from this process, in terms of the unfolding of the rich potentialities of the human species, are to be perpetuated and increased, conversion to a negative feedback system, through which a viable homeostatic (not static) stability can be achieved, is essential—otherwise the system will self-destruct. The present concerns with dehumanization in a technicized society, with the degradation of the quality of the human ecosystem, and with the quality of human life may be cybernetic signals that, hopefully, will trigger the conversion.

Viewing the human mind as an integral part of a new, higher-order ecosystem need not detract from the humanistic attributes of man, by reducing human society to a systems structure and behavior comparable to that of the lower levels of organized systems. Indeed, the uniqueness of the human ecosystem lies in the creativity of man, through

which new integral configurations emerge. The human ecosystem is a new and unique systems level of organization for the planet Earth. The current crisis lies in the threat of destroying the integrity of the world ecosystem as a life-support system through inadvertent, destructive modifications of the system. An understanding of ecosystem processes at the level of the total human ecosystem is needed, as a basis for bringing the system into functional harmony through technology, which is essential if the system is to be conducive to evolution of the noosphere toward the full potential of the human species. In today's world, the noosphere may be looked upon as the free systems dynamics of the human ecosystem, through which the system can adapt to the revolutionary changes brought on by the cultural evolution of man.