Ecosystems☆

Brian D Fath, Towson University, Towson, MD, United States and International Institute for Applied Systems Analysis, Laxenburg, Austria

Introduction

Ecology is a broad and diverse field of study. One basic distinction in ecology is between autecology and synecology, in which the former considers the ecology of individual organisms and populations, mostly concerned with the biological organisms themselves; and the latter, the ecology of relationships among the organisms and populations, which is mostly concerned with communication of material, energy, and information of the entire system of components. In order to study an ecosystem, one must have knowledge of the individual parts; thus, it is dependent on fieldwork and experiments grounded in autecology. However, the focus is much more on how these parts interact, relate to, and influence one another including the physical environmental resources on which life depends. Ecosystem ecology, therefore, is the implementation of synecology. In this manner, the dimensional units used in ecosystem studies are usually the amount of energy or matter moving through the system. This differs from population and community ecology studies in which the dimensional units are typically the number of individuals (**Table 1**).

History of the Ecosystem Concept

The term ecosystem, which is ubiquitous today, both as scientific terminology and in common vernacular, was first used by Arthur Tansley in 1935 in a seminal paper in the journal *Ecology*, entitled "The use and abuse of vegetational concepts and terms." In fact, his reason for coining the term "ecosystem" was in response, as the title says, to a perceived abuse of community concepts by some, such as Clements, Cowles, and Phillips, who interpreted an ecological community as having overt organismal-like properties. The community as organism metaphor bothered Tansley to the extent that he wanted to provide a more scientific footing for the processes and interactions occurring during community development. Tansley describes the ecosystem thusly, "…the fundamental conception is… the whole system, including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense." The definition he proposed over 80 years ago sounds fresh today, since it has changed little if at all. The major tenets of this approach are the explicit inclusion of nonliving processes interacting with the biota—in this sense it is more along the Haeckelian lines of ecology than the Darwinian, with an additional emphasis on the system. The latter tied the field closer to the burgeoning disciplines of general system theory and system analysis, and later complex systems theory and socio-ecological metabolism.

While the conceptual underpinning of the ecosystem was now established, the introduction of this term was theoretical, lacking guidance as to how it might be applied as a field of study. There were around this time several whole system energy budgets being developed, particularly for lake ecosystems by North American ecologists such as Juday and Birge in Wisconsin, which were ideal test cases for the ecosystem concept. Building on this work, in 1942, Lindeman's study of Cedar Bog Lake also in Wisconsin was published, providing, for the first time, a clear application of the ecosystem concept. In addition to constructing the food cycle of the aquatic system, he developed a metric—now called the Lindeman efficiency—to assess the efficiency of energy movement from one trophic level to the next based on ecological feeding relations. His conceptual model of Cedar Bog Lake included passive flows to detritus, but these were not included in the trophic enumeration. Since then numerous additional studies have followed this same approach, applying it to many habitats such as terrestrial, aquatic, and urban ecosystems.

Defining an Ecosystem

As stated above, an ecosystem is comprised of the ecological community and its interactions with the nonliving environment. This is often referred to as the interaction of the biotic and abiotic aspects of the ecosphere, however, the term abiotic does a disservice to the overwhelming influence that life has on the planet it inhabits. Many examples of feedback and biotic conditioning of the environment exist such as soil formation and erosion, an oxygen atmosphere and the protective ozone layer, and a balanced carbon cycle. Even simple factors such as temperature, humidity, and soil pH are biologically-mediated leading one to consider that a better term for these features is *conbiotic* rather than abiotic (see entry in this volume). An ecosystem, as a unit of study, must be a bounded system, yet the scale can range from a puddle, to a lake, to a watershed, to a biome. Indeed, ecosystem scale is defined more by the functioning of the system than by any checklist of constituent parts and the scale of analysis should be determined by the problem being addressed. Whereas, individuals perish over time, and even populations cannot survive indefinitely—none can fix their own energy and process

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Table 1 Typical dimensional units of study at different ecological scales

Ecological scale	*Dimensions*
Organismal ecology	dE/dt
Population ecology	dN/dt
Community ecology	dN/dt
Ecosystem ecology	dE/dt

dE/dt, change in energy over time; dN/dt, change in number over time.

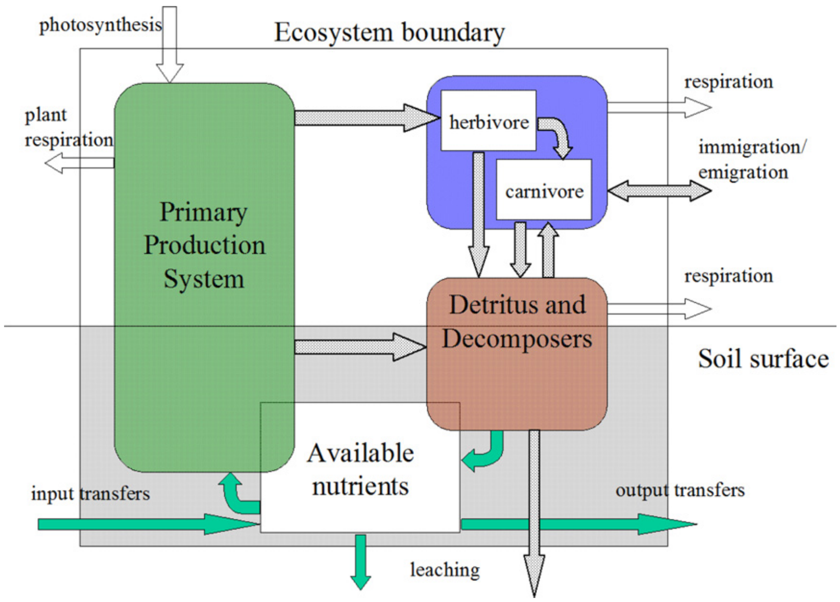

Fig. 1 Conceptual diagram of a simplified ecosystem.

their own wastes—every ecosystem contains the ecological community necessary for sustaining life: primary producers, consumers, and decomposers, and the physical environment for oikos (**Fig. 1** shows a simple ecosystem model). It is this feature of ecosystems, that they are the basic unit for sustaining life over the long-term, which provides one of the main reasons for studying them for environmental management and conservation. The two main features of the ecosystem, energy flow and nutrient biogeochemical cycling, comprise the major areas of ecosystem ecology research.

Energy Flow in Ecosystems

The thermodynamic assessment of an ecosystem starts with the recognition that an ecosystem is an open system, in the sense of physics, such that it receives energy and matter input from outside its borders and transfers output back to this environment. Thus, every ecosystem has a system boundary and is embedded in an environment that provides low-entropy energy input and can receive high-entropy energy output. In addition to the external resource source–sink, there is another internal, within system boundary environment with which each organism directly and indirectly interacts. Patten proposed the concept of these two environments, one external and mostly unknowable—other than the input–output interactions, and the second internal and measurable—that is, external to the specific organismal component but within system boundary, as a systems approach to quantify indirect, yet within system interactions. This approach—called environ analysis—relying on the methodologies of input–output analysis, has developed into a powerful analysis tool for understanding complex interactions and dependencies in ecological networks. For now though, let us concern ourselves more generally with what occurs within the ecosystem boundary.

Energy flow in ecosystems begins with the capture of solar radiation by photosynthetic processes in primary producers. (Note, there are also chemoautotrophs that capture energy in the absence of sunlight, but while biologically fascinating, contribute negligible energy flux to the overall global ecological energy balance. Their significance may be in being evolutionarily earlier forms of energy capture.)

$$\text{Energy} + 6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2 \quad (1)$$

The accumulated organic matter, first as simple sugars then combined with other elements to more complex molecules, represents the gross primary production in the system, some of which is released and used for the primary producers' growth and maintenance through respiration.

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{Energy} \quad (2)$$

The reminder, or net primary production is available for the rest of the ecosystem consumers including decomposers. Secondary production refers to the energetic availability of the heterotrophic organisms, which accounts for the energy uptake by heterotrophs and the energy used for their maintenance. Overall ecosystem production is supported by the primary producers, whereas ecosystem respiration includes the metabolic activity of all the ecosystem biota (Table 2). In this manner, plants provide the essential energetic-basis for all ecological food webs. Since it is often difficult to make direct measurements of ecological production, the change in biomass growth can be used as representative of production.

The captured energy moves through a reticulated network of interactions forming the complex dependency patterns known as food webs. In a simplified food chain, and as first described by Lindeman, the trophic concept is used to assess the distance away from the original energy importation, but in reality the multiple feeding pathways found in ecological food webs make discrete trophic levels a convenient yet inaccurate simplification. Elton observed that one typically finds a decreasing number of organisms as one proceeds up the food chain from primary producers to herbivores, carnivores, and top carnivores—leading him to propose a pyramid of numbers. One can control for the individual variation in body size by considering the biomass at each trophic level rather than the number of individuals—resulting in a pyramid of biomass. The trophic pyramid is a thermodynamically satisfying view of interactions since according to the Second Law energy must be lost during each transformation step; plus energy is used at each level for the maintenance of that level. Under this paradigm, the trophic levels apparently cap out around five or six levels. Fractional trophic levels have been employed to account for organisms feeding at multiple levels, but even these do not usually account for the role of detritus and decomposition, which extend the feeding pathways to higher numbers. However, instead of linking detritus as a source compartment in the ecosystem conceptual model, the standard paradigm is to envision two parallel food webs one with primary producers as the base, and the other with detritus as the base without any input from the rest of the web. If detritus were properly linked as both a source and sink in the ecosystem, then it would be clear that longer energy pathways are possible, if not common. The longer energy flow pathways observed in some studies are not in conflict with the laws of thermodynamics, but they show that ecosystems are more thorough at utilizing the energy within the system, mostly by decomposers, before it is lost as degraded, unavailable energy.

Energy resources flowing through the ecosystem are necessary to maintain all growth and development activities. Organisms follow a clear life history pattern, and while the time scales differ depending on the species, early-stage energy availability is usually used for growth, while later energy surplus is used for maintenance or reproduction. A similar pattern is visible in ecosystem-level growth and development. Net primary production is used to build biomass and physical structure of the ecosystem. The additional structure of photosynthetic material allows for the additional import of solar energy until saturation is reached at about 80% of the available solar radiation. At this point, the overall growth of the ecosystem begins to level off because although gross primary production is high, the overall system supports more and more nonphotosynthetic biomass both in terms of nonphotosynthetic plant material and heterotrophs. When the average gross production is entirely utilized to support and maintain the existing structure, net production is zero and the system has reached a steady state regarding biomass growth. However, the ecosystem continues to develop both in terms of the network organization and in the information capacity. In addition to being a dynamic steady state, it does not persist indefinitely because disturbances afflict the system setting it back to earlier successional stages in which the growth and development processes begins anew, possibly with different results. In this manner, the disturbance acts according to Holling's creative destruction (see entry on Holling Cycle) providing the system the opportunity to develop along a different pathway. Recent work on ecosystem growth and development has focused on the orientation of thermodynamic indicators such as energy throughflow, energy degradation, biomass, work energy capacity, and specific entropy. These orientors provide good system-level indicators of development during succession or restoration of impaired ecosystems.

Biogeochemical Cycles

A useful adage to remember regarding ecosystems is that there are no trashcans in nature. All material is source for some other process. Therefore, another major focus of ecosystem ecology is understanding how the chemical elements necessary for life persist and translocate in pools and fluxes within the ecosphere. The biosphere actively interacts with the three nonliving spheres (hydrosphere, atmosphere, and lithosphere) to provide the available concentration of each for life. This action has a significant impact on the relative distribution of these elements. The simple sugar products of photosynthesis, $C_6H_{12}O_6$, are the base for organic matter so carbon, hydrogen, and oxygen dominate the composition of life, and while oxygen is available in the

Table 2 Ecosystem energetics defined by net and gross production

Net primary production = gross primary production − respiration (autotrophs)
Net secondary production = gross secondary production − respiration (heterotrophs)
Net ecosystem production = gross primary production − ecosystem respiration (autotrophs + heterotrophs)
Net production = biomass (now) − biomass (before)

lithosphere, and hydrogen in the hydrosphere, carbon is actually quite scarce in the environment, making the disproportionate amount of carbon in biomass a hallmark of life. In fact, there are about 20 elements used regularly in living organisms, of which 9 are called the macronutrients as the major constituents of organic matter: hydrogen, oxygen, carbon, nitrogen, calcium, potassium, silicon, magnesium, and phosphorus. Some of these elements are readily available in the abiotic environment, in which case conservation through cycling of the elements is not paramount, however those in scarce supply, such as nitrogen and phosphorus, are reused many times before being released from the system (**Table 3**). These biogeochemical cycles provide the foundation to understand how human modification leads to eutrophication (N and P cycles) and global climate change (C cycle). Therefore, much effort has been made to study and understand these cycles, particularly the carbon, nitrogen, and phosphorus cycles, details of which are addressed elsewhere in this encyclopedia.

Ecosystem Studies

The ecosystem perspective achieved footing in the ecological academic community since it was central to Gene Odum's seminal textbook *Fundamentals of Ecology* first published in 1953. An early implementation of this approach at the institutional scale was attempted was in the International Biological Program (IBP), which was run from 1964 to 1974. The program had many successes in assessing and surveying the earth's ecosystems, but faced the difficulty of compelling a top–down, holistic research paradigm on individual scientific endeavors. As a result of this conflict, the program did not deliver as much as had been hoped, but set the stage for the next generation of ecosystem-scale research. One feature of the IBP that did continue was the use of computer simulation modeling as a tool to understand the complex ecological interrelations. The journal, *Ecological Modeling and Systems Ecology*, was started in 1975 and continues as an active outlet for mathematical and computer-based ecosystem research.

Subsequent to the IBP, the U.S. National Science Foundation officially established the Long-term Ecological Research Sites (LTER) in 1980 but research at several of the sites dates much earlier. Currently, there are 30 such sites ranging from the Coweeta Hydrological Lab in North Carolina, Hubbard Brook Ecosystem Study in New Hampshire, Sevilleta National Wildlife Refuge in New Mexico, and the Baltimore Ecosystem Study (lternet.edu/lter-sites). These projects rely on a vast team of scientists to study the many interactions at this spatial scale. Still, the difficulty lies in putting together all the pieces into an integrated whole picture of the ecosystem.

Smaller-scale, individual-led ecological research is commonly conducted using microcosm and mesocosm experiments. A mesocosm experiment uses designed equipment or enclosures in which environmental factors can be controlled and manipulated to approximate natural conditions. The prevalence of this approach created a wealth of small-scale experimentation but at the expense of larger observational studies, which sparked a fierce debate in the 1990s between the "field" versus "bottle" approach. Indeed, the usefulness of microcosm experiments for ecosystem ecology was brought into question, but the resolution has been that a multiplicity of approaches is useful to address ecological questions.

Biomes

Specific ecosystem characteristics are variable across the globe depending on the location and conditions. Tansley discussed in detail the factors that go into forming a climax community such as edaphic or physiographic. A simple formulation considers the regions' climatograph, a combination of temperature and precipitation and from those two variables gives a good indication of the terrestrial ecosystem (**Table 4**). These climatic conditions determine whether the regions are tropical or temperate, trees or grasses, providing a rich display of ecosystems across the globe.

Human Influence on Ecosystems

Humans have greatly altered and impacted the global biosphere. We recognize now the importance of maintaining functioning ecosystem services both out of our own necessity and for the obligation we have to the ecosphere. In 2000, the United Nations

Table 3 Percentage atomic composition of the biosphere, hydrosphere, atmosphere, and lithosphere for first 10 elements

Biosphere		*Hydrosphere*		*Atmosphere*		*Lithosphere*	
H	49.8	H	65.4	N	78.3	O	62.5
O	24.9	O	33.0	O	21.0	Si	21.22
C	24.9	Cl	0.33	Ar	0.93	Al	6.47
N	0.073	Na	0.28	C	0.04	H	2.92
Ca	0.046	Mg	0.03	Ne	0.002	Na	2.64
K	0.033	S	0.02			Ca	1.94
Si	0.031	Ca	0.006			Fe	1.92
Mg	0.030	K	0.006			Mg	1.84
P	0.017	C	0.002			K	1.42

Table 4 Basic characteristics of major terrestrial biomes

Biome	*Precipitation (cm)*	*Temperature (°C)*
Tundra	<25	−12
Taiga	35–100	10
Temperate deciduous forest	75–150	0–30
Temperate rain forest	200–400	9–12
Tropical rain forest	200–600	25
Desert	<25	35
Grassland	25–75	9–25

Table 5 A few of the tends identified in the Millennium Ecosystem Assessment

50% of all the synthetic nitrogen fertilizer ever used has been used since 1985	20% of the world's coral reefs were lost and 20% degraded in the last several decades
60% of the increase in the atmospheric concentration of CO_2 since 1750 has taken place since 1959	35% of mangrove area has been lost in the last several decades
Approximately 60% of the ecosystem services evaluated are being degraded or used unsustainably	Withdrawals from rivers and lakes doubled since 1960

Table 6 Ecosystem approach principles of the convention on biological diversity

The following 12 principles are complementary and interlinked
Principle
1 The objectives of land, water, and living resource management are a matter of societal choices
2 Management should be decentralized to the lowest appropriate level
3 Ecosystem managers should consider the effects (actual or potential) of their activities on adjacent and other ecosystems
4 Recognizing potential gains from management, there is usually a need to understand and manage the ecosystem in an economic context. Any such ecosystem-management program should:
(a) Reduce those market distortions that adversely affect biological diversity
(b) Align incentives to promote biodiversity conservation and sustainable use
(c) Internalize costs and benefits in the given ecosystem to the extent feasible
5 Conservation of ecosystem structure and functioning, in order to maintain ecosystem services, should be a priority target of the ecosystem approach
6 Ecosystem must be managed within the limits of their functioning
7 The ecosystem approach should be undertaken at the appropriate spatial and temporal scales
8 Recognizing the varying temporal scales and lag-effects that characterize ecosystem processes, objectives for ecosystem management should be set for the long term
9 Management must recognize the change is inevitable
10 The ecosystem approach should seek the appropriate balance between, and integration of, conservation and use of biological diversity
11 The ecosystem approach should consider all forms of relevant information, including scientific and indigenous and local knowledge, innovations, and practices
12 The ecosystem approach should involve all relevant sectors of society and scientific disciplines

Secretary General called for a global ecological assessment, which was recently published as the Millennium Ecosystem Assessment (MEA) (www.maweb.org/en/index.aspx). The report compiled by over 1350 experts from 95 countries found that humans have changed ecosystems more rapidly and extensively over the last 50 years than in any comparable period of time in human history, resulting in a substantial and largely irreversible loss in the diversity of life on Earth (other highlights from the report are presented in **Table 5**). The MEA operated within a framework that identified four primary ecosystem services needed by humans: supporting (nutrient cycling, primary production, soil formation, etc.), provisioning (food, water, timber, fuel, etc.), regulating (climate, flood, disease, etc.), and cultural (aesthetic, spiritual, educational, recreational, etc.). All have shown signs of stress and human pressures during the past century. One positive trend was the increase in food production (crops, livestock, and aquaculture), but this occurred with a concomitant loss of wild fisheries and food capture, along with a substantial increase in the resource inputs required to maintain the high agricultural production. While these observed changes to ecosystems have contributed to substantial net gain in human well-being and economic development, they have come at an increasing cost to the ecosystem health. The loss of this natural capital is typically not properly reflected in economic accounts.

Since the ecosystem provides the necessary functions for life, environmental management principles being devised and implemented today use the ecosystem concept as foundation. In particular, there have been several high profile international efforts such as with the Convention on Biological Diversity (CBD), a treaty initiated in 1992 and signed by 150 government leaders with the express aim to protect and promote biological diversity and sustainable development. The *Ecosystem Approach* adopted within this convention uses scientific methodologies regarding ecological interactions among organisms, their environment, and human activity to promote conservation, sustainability, and equity for managing natural resources. The approach deals with the complex socio-ecological-economic systems by promoting integrated assessment and adaptive management (see entry on Panarchy). The Ecosystem Approach of the CBD is outlined below in 12 principles (**Table 6**). Note particularly principles 5–8 that deal with ecosystem functioning, and taken in the context of the other principles assert how this ecological functioning provides opportunities and constraints for economic and social well-being. Better understanding these issues, such as ecosystem services, scale, time-lags, and dynamics are paramount research areas today.

At a national scale, in the United States, the Endangered Species Act of 1973 was critical legislation that puts into place a recovery plan for any species listed as endangered or threatened. What is impressive is that the legislation rests firmly on an ecosystem approach when it states: "The purposes of this Act are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved…" This holistic approach was already evident in the Organic Act of 1916, which codified the process of designating National Parks (the first, Yellowstone, was established in 1872) with the "purpose is to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." The US Wilderness Act of 1964 provided additional protection to natural places stating they are areas "where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain". It is encouraging to see scientific understanding and perspective referenced in legislation. Unfortunately, all of these protections are under threat from politics and businesses that undervalue ecosystems and their services.

Summary

Ecosystems are a unit of organization that include the interactions of the ecological community with its nonliving environment, primarily in terms of the energy flow and nutrient cycling. Research in ecosystem ecology has given us a much better understanding of the processes and functions necessary to sustain life. The work in the natural sciences has outpaced the ability of the social institutions to adapt and implement this knowledge. However, there is reason to be optimistic because the recent focus on the ecosystem approach in major international efforts recognizes that humans, with their cultural diversity, are an integral component of ecosystems.

See also: **Conservation Ecology:** Protected Area. **Ecological Data Analysis and Modelling:** Conceptual Diagrams and Flow Diagrams. **Evolutionary Ecology:** Red Queen Dynamics; Metacommunities. **General Ecology:** Keystone Species and Keystoneness; Seed Dispersal; Temperature Regulation. **Terrestrial and Landscape Ecology:** Ecological Engineering: Design Principles

Further Reading

Chapin III, F.S., Matson, P.A., Vitousek, P.M., 2010. Principles of terrestrial ecosystem ecology, 2nd edn New York: Springer, p. 529.
Fath, B.D., Jørgensen, S.E., Patten, B.C., Straškraba, M., 2004. Ecosystem growth and development. Biosystems 77, 213–228.
Golley, F.B., 1993. A history of the ecosystem concept in ecology. New Haven, CT: Yale University Press.
Jørgensen, S.E., Fath, B.D., Bastianoni, S., Marques, J.C., Müller, F., Nielsen, S.N., Patten, B.C., Tiezzi, E., Ulanowicz, R.E., 2007. A new ecology: Systems perspective. Amsterdam: Elsevier, p. 275.
Likens, G.E., Borman, F.H., Johnson, N.M., Fisher, D.W., Pierce, R.S., 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecological Monographs 20, 23–47.
Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–418.
Odum, H.T., 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs 27, 55–112.
Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.
Patten, B.C., 1978. Systems approach to the concept of environment. The Ohio Journal of Science 78, 206–222.
Raffaelli, D.G., Frid, C.L.J., 2010. Ecosystem ecology: A new synthesis. Cambridge: Cambridge University Press, p. 173.
Tansley, A.G., 1935. The use and abuse of vegetational concepts and terms. Ecology 16, 284–307.
Weigert, R.G., Owen, D.F., 1971. Trophic structure, available resources and population density in terrestrial versus aquatic ecosystems. Journal of Theoretical Biology 30, 69–81.