Ecosystem Ecology

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Introduction

Ecosystem ecology is a branch of study and thinking within the ecological sciences that focuses on the ecosystem – a dynamic complex of interactions of organisms and their environment - and the importance of these interactions to the organisms and earth system processes. The discipline represents one of two different episthomological approaches within ecology that emerged in the 20th century - a species-centric community-based approach and a process-centric ecosystem-based approach. Both approaches study the ways in which species interact among themselves and their environment, share a common language, and a common set of principles. The community-based approach focuses on how species distributions and abundances are shaped by their resource needs and tolerances to environmental conditions and by their interactions with other species. The ecosystem-based approach represent a significant departure in that it considers the resource needs and tolerances of species and their interactions with other species as well, but factors in the contributions species make to earth system processes (e.g., biogeochemical cycles, climate). The two perspectives are not as mutually exclusive as the phrasing of the approaches suggests, but rather offer different approaches to how we view the environment and communities and the factors that regulate them. In the 21st century, modern ecosystem science includes the influences that humans have as part of ecological communities, and as drivers of change in ecological communities. This linkage within the ecosystem perspective of biology affecting the physical environment, and the recent developments that include the social and human dimensions have positioned the approach as being critical to understanding the relationship among global processes and the services that ecosystems provide to human well-being that is embodied in the emerging science of sustainability.

Journals

Given the broad appeal of ecosystem science as a discipline, concept and approach, articles in the field appear in numerous (>100) journals that appeal to the scientific community as a whole, and the ecological community, journals that specialize in different ecosystem types, topics and fields, and journals that focus on the emerging field of sustainability science. Highly-rated journals of general scientific and societal interest include *Bioscience*, *Nature*, *Science*, *Proceedings of the National Academy of Sciences*, and *Proceedings of the Royal Society B*. Top-ranked ecological journals include journals published by the British Ecological Society (*Functional Ecology, Journal of Animal Ecology, Journal of Applied Ecology, Journal of Ecology*), The Ecological Society of America (*Ecology*, *Ecological Applications*, *Ecological Monographs*, *Ecosphere, Frontiers in Ecology and the Environment*), and Annual Reviews (*Annual Reviews of Ecology and Evolution*, *Annual Reviews of Entomology*), as well as *Ecology Letters*, *Ecosystems,* and *Trends in Ecology and Evolution*. Journals specializing in different fields and topics include but not limited to *Global Change Biology*, *Landscape Ecology*, *Nature Climate Change*. Journals within the field of sustainability include *Ecosphere*, and *Ecosystem Health and Sustainability*.

Annual Review of Ecology, Evolution, and Systematics [http://www.annualreviews.org/journal/ecolsys]

Published by Annual Reviews the journal, along with discipline and topic specific companion journals in the series publishes significant developments in the fields of ecology, evolutionary biology, and systematics. The reviews cover many topics germane to ecology in general and ecosystem ecology from ecosystems processes, conservation, and environmental management.

BioScience [https://www.aibs.org/bioscience/]

Published by the American Association for the Advancement of Science. Articles include current research and essay in biology, education, public policy, and history.

Ecology [http://esajournals.onlinelibrary.wiley.com]

Published by the Ecological Society of America. The journal publishes articles, comments and reviews on basic and applied ecology, many from the ecosystem science perspective.

Ecology Letters [http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1461-0248]

A publication of the French National Center for Scientific Research (CNRS). The journal publishes research articles in ecology.

Ecological Applications [http://esajournals.onlinelibrary.wiley.com]

Published by the Ecological Society of America. The journal published articles, comments and reviews on the ecological science to environmental challenges that develop scientific principles to support environmental decision-making, and discuss the application of ecological concepts to environmental issues, policy, and management.

Ecological Monographs [http://esajournals.onlinelibrary.wiley.com]

Published by the Ecological Society of America. The journal published articles that provide comprehensive documentation of major advances in the field and that establish benchmarks from which future research will build.

Ecosystem Health and Sustainability [http://esajournals.onlinelibrary.wiley.com/]

Published by the Ecological Society of America and the Ecological Society of China. The journal published articles, comments and reviews on publishes articles on advances in macroecology and sustainability science, on how changes in human activities affect ecosystem conditions, and on systems approaches for applying ecological science in decision-making to promote sustainable development.

Ecosphere [http://esajournals.onlinelibrary.wiley.com]

Published by the Ecological Society of America. The journal is an open access journal intended to provide rapid publication of articles, comments and reviews on a broad range of ecology and ecology-related topics including interdisciplinary studies relating to ecology.

Ecosystems [http://link.springer.com/journal/10021]

The journal publishes articles in ecosystem ecology ranging from fundamental ecology, environmental ecology and environmental problem-solving. Topics include but are not limited to ecology, plant sciences, zoology, environmental management Geoecology/natural processes, and hydrology/water resources.

Frontiers in Ecology and the Environment [http://esajournals.onlinelibrary.wiley.com/]

Published by the Ecological Society of America. The journal published articles, comments and reviews on a broad range of ecology topics, the environment, and related disciplines with broad interdisciplinary appeal.

Functional Ecology [http://www.britishecologicalsociety.org/publications/journals/functional-ecology/]

Published by the British Ecological Society. The journal publishes high-impact papers on ecological patterns and processes from the organismic to the ecosystem scale.

Global Change Biology [http://onlinelibrary.wiley.com/journal/]

This highly regarded and cited journal publishes articles that focus the integration of aspects of current environmental change on a global and biological systems.

Journal of Animal Ecology [http://www.britishecologicalsociety.org/publications/journals/journal-of-animal-ecology/]

Published by the British Ecological Society. The journal publishes original research on all aspects of animal ecology, ranging from the molecular to the ecosystem level from utilizing terrestrial, freshwater or marine systems.

Journal of Applied Ecology [http://www.britishecologicalsociety.org/publications/journals/journal-of-applied-ecology/]

Published by the British Ecological Society. The journal publishes on the interface between ecological science and the management of biological resources. Relevant themes include conservation biology, global change, land use and management, and restoration ecology.

Journal of Ecology [http://www.britishecologicalsociety.org/publications/journals/journal-of-ecology/]

Published by the British Ecological Society. The journal publishes original papers on the ecology of plants in both aquatic and terrestrial ecosystems.

Landscape Ecology [http://link.springer.com/journal/10980]

The journal focus on the ecology of spatial heterogeneity including basic and applied research on ecosystem services and the sustainability of coupled human-environmental systems.

Nature [http://www.nature.com/nature/journal]

A highly regarded weekly international journal that publishes a wide range of scientific articles, including those of basic and applied ecosystem ecology.

Nature Climate Change [http://www.nature.com/nclimate]

Published by Nature Research, this journal publishes original research articles, opinions and reviews on the changes to Earth's climate and the consequences of those changes.

Proceedings of the National Academy of Sciences [http://www.pnas.org]

Published by the US National Academy of Sciences, this highly regarded journal publishes research across the sciences spanning the biological, physical and social sciences.

Proceedings of the Royal Society B [http://rspb.royalsocietypublishing.org]

Published by the Royal Academy, the journal presents research articles and reviews of broad general interest in biology, including general ecology, ecosystem ecology, and global change biology.

Science [http://science.sciencemag.org]

A publication of the American Association for the Advance of Sciences. Science is a weekly international journal that publishes high-impact papers from all aspects of science including ecosystem ecology.

Soil Biology and Biochemistry [https://www.journals.elsevier.com/soil-biology-and-biochemistry]

The journal publishes research articles on biological processes in soil. Topics include issues of soil and environmental quality and the understanding of the role of soil biology and biochemistry in mediating soil functions, agricultural sustainability and ecosystem services.

Trends in Ecology and Evolution (TREE) [http://www.cell.com/trends/ecology-evolution/aims]

Publishes reviews, opinions and letters in all areas of ecology and evolutionary science from basic to applied research and from molecular to global scales. Provides excellent synopses of important issues concerning organisms and their environments.

Ecosystem Structure - Boundaries

There are several variations to the definition of ecosystem ecology, all of which include the study of organisms and their interaction within their physical environment. Within ecosystem ecology defining their boundaries can be a challenge as they are dependent on the spatial and temporal scale of interest and to questions being asked. Post et al. (2007) provides a review and overview of the structural and functional criteria that are used to establish the boundaries of an ecosystem. At the global scale, the earth can be viewed as an ecosystem, open to energy and largely closed to matter. At smaller scales ecosystems are open to both energy and matter, and are defined in terms terrestrial and aquatic features, dominant vegetation types, assemblages of organisms, climate, geologic history, biogeography, soil types, or habitat characterizations. For terrestrial ecosystems, the commonly used life zone (Holdridge 1947) and biome (Whittacker 1975) concepts of characterizing ecological communities are based on climate (temperature and precipitation) and the dominant vegetation types. Turner (2015) argues that landscapes – expanses of land and water – have also served as boundaries for ecosystems, or collections of ecosystems. Ellis and Ramankutty (2008) introduced the idea that urban centers should be now classified as anthropogenic biomes. At finer scales, biomes are often sub-divided into smaller units of study. Freshwater and Marine ecosystems are often subdivided into littoral, pelagic and benthic zones. Coleman et al. (2004) note that soils are subdivided along the litter layer, lower soil horizons, or the region around roots (aka the rhizosphere).

Ellis, E.C. and Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment 6: 439-447.

The authors introduce the concept of the Anthropogenic Biomes – a characterization of terrestrial biomes based on global patterns of sustained, direct human interaction with ecosystems. An important paper in the ongoing evolution of Scoial-Ecology.

Coleman, D.C., Crossley, Jr., D., and Hendrix, P.F. (2004), Fundamentals of Soil Ecology. 2^{nd}, Ed.Elsevier Academic Press, New York, NY, 408 pages. doi.org/10.1016/B978-012179726-3/50007-1.

An excellent text on soil biology and ecosystem structure and function.

Holdridge, L.R. (1947) Determination of world plant formation from simple climate data. Science 105: 367-368.

The paper that established the concept of life zones to categorize ecosystems.

Post, D.M., Doyle, M.W., Sabo, J.L., and Finlay, J.C. (2007). The problem of boundaries in defining ecosystems: A potential landmine in uniting geomorphology and ecology.

An excellent review of the criteria used and their scale-depend nature to define the boundaries of ecosystems.

Turner, M.G. and Gardner, R.H. (2015). Landscape Ecology in Theory and Practice. Springer-Verlag, New York, NY, USA.

A modern and thorough treatment of the field of landscape ecology from the ecosystem perspective. This is an important advancement as it incorporates current social-ecological thinking.

Whittaker, R.H. (1975). Communities and Ecosystems. 2^{nd} Edition, MacMillan, New York, NY.

A compilation of the Biomes of the world.

Ecosystem Structure - Biodiversity

Biodiversity refers to more than the number of species as it characterizes the variation and variety of life at the genetic, species and ecosystem level. These characterizations are important as they provide the framework from which to study the relationships between ecosystem structure, function, and dynamics. Cleland (2011) and Moore (2013) provide reviews of the criteria that ecosystem ecologist have used to study biodiversity. For certain questions and scales individual species are used, but often the system is described in terms of species grouped into larger units. The schemes used have ranged from ones of convenience, which are usually based on a broad taxonomic category, to ones that have adopted strict criteria such as resource-use or functional traits that may include organisms from different taxonomic groupings. Naeem et al. (1994) provide an important paper on the relationship between ecosystem biodiversity and ecosystem function. Loreau et al. (2002) provide an excellent compilation of work that ensued on the relationship between diversity and function is provided in the edited volume. Tilman and Downing (1994) take this idea further by demonstrating that for plant communities, diversity, function (as measured by productivity), and stability (as measured by recovery from drought) were inter-related, arguing that biodiversity was important to maintaining stable rates of productivity in ecosystems. McCann (2000) reviews the relationship between the biodiversity of an ecosystem and its dynamic stability. Hoeksema et al. (2010) present a comprehensive meta-analysis on the impact of mycorrhizal fungi on plant growth, local biodiversity and ecosystem function.

Cleland, E.E. (2011). Biodiversity and ecosystem stability. Nature Education Knowledge 3:14.

A nice summary of the criteria used to define ecosystem biodiversity and how the information can be used to study ecosystem function and dynamics.

Hoeksema, J.D., Chaudhary, V.B., Gerhing, C.A., Johnson, N.C., Karst, J., Koide, R.T., Pringle, A., Zabinski, C., Bever, J.D., Moore, J.C., Wilson, G.W.T., Klironomos, J.N., and Umbabhower, J. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhical fungi.

A thorough and interesting meta-analysis of field and laboratory studies on the effects of N additions to mycorrhizal associations. The demonstrates the importance of mycorrhizae to the biodiversity and function of ecosystems.

Loreau, M., Naeem, S. and Inchausti, P. (2002). Biodiversity and Ecosystem Functioning, Eds. Oxford University Press, Oxford, UK. 294 pages.

An excellent compilation of papers that address different aspects of the relationship between biodiversity and ecosystem function.

McCann, K.S. (2000). The diversity-stability debate. Nature 405: 228-233.

An excellent review of diversity-stability relation debate

Moore, J.C. 2013. Biodiversity, taxonomic verses functional. *In:* Encyclopedia of Biodiversity 2nd Edition. S. Levin (Ed.), Elsevier, Oxford, pp. 648-656.

A review of different ways to categorize biodiversity to ecosystem processes.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. , and Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. Nature 368: 734-737.

A seminal paper that proposed a that ecosystem function was inextricably inter-related to its biodiversity/

Tilman, D. and Downing, J.A. (1994). Biodiversity and stability in grasslands. Nature 367: 363-365.

A seminal paper demonstrating the inter-relationship among ecosystem structure, functional and dynamics.

Ecosystem Processes - Basic Principles

The textbooks by Odum (1953) and Chapin et al. (2011) among others provide detailed accounts of fundamental ecosystem processes – production, decomposition, mineralization, immobilization – within the context of biogeochemical cycles. Ecosystem processes encompass the transformations of materials and flow of energy from biotic and abiotic pool or states to another. Biotic pools can be living or non-living represented by organisms and their byproducts (e.g., corpses, unconsumed prey and leavings, feces). Abiotic components include but not limited to the atmosphere, bodies and expanses of liquid and frozen water, and the chemical and physical components of soils and water. A biogeochemical cycle describes the pathway that a chemical substance moves through the biotic and abiotic components of the earth system. There are several biogeochemical cycles that are of interest to ecosystem scientists, but the primary cycles are the carbon cycle, nitrogen cycle, phosphorous cycle, sulfur cycle and water cycle. Hutchinson (1948) provides the foundational account of the relationship of biogeochemical cycles to the ecosystem concept. Ecosystem processes can be discussed in the simplest terms of the input and output of energy of driving immobilization - the transformation of substance from an inorganic form to an organic form – and mineralization - the transformation of a substance from an organic form to an inorganic form as represented in familiar chemical equilibrium representation of photosynthesis and respiration $6CO_2 + 6H_20 \leftrightarrow C_6H_{12}O_6 + 6O_2$.

Biogeochemical cycles do not operate in isolation and are often inter-related and dependent on one another, due in part to the finite nature (read limiting) of resources, thermodynamic constraints, and the coupled dependency of cycles (ecological stoichiometry). Much of the work that followed tended to be either descriptive in nature, studying the factors that regulate production and decomposition, cataloging the sources and sinks of key moieties, experimental treatments studying the consequences of altering the abundances of nutrients on plant growth and ecosystem process, studies designed to understand regulators of biogeochemical cycles within ecosystems. Contemporary treatments of biogeochemical cycles cover much of the earlier work by including detailed synopses of their descriptions and the factors that regulate them, how they interact with one another, how human activity has affected them, and how changes in the cycles affect ecosystem structural, functional, and dynamic properties. Schlesinger and Bernhardt (2013) provide a thorough basic stand-alone text on biogeochemical cycles, their interactions, and the effects of humans on them. Chapin et al. (2011) provides an in depth account of ecosystem processes and the dominant biogeochemical cycles in their text entitled the Principles of Terrestrial Ecology. Sterner and Elser (2002) present a comprehensive treatment of ecological stoichiometry - the coupled dependency of biogeochemical cycles and energetics on organisms and ecosystems.

Chapin, S. F. III, Matson, P.A., and Vitousek, P.M. 2011. Principles of Terrestrial Ecosystem Ecology.

> This general text in ecosystem ecology provides excellent overviews of the major biogeochemical cycles, how human activity alters them, and the consequences of these alterations on ecosystems and ecosystem services.

Hutchinson, G.E. (1948). Circular Causal Systems in Ecology. Annals of the New York Academy of Sciences 50:221-246.

An important paper that lays out the framework for what became the model ecosystem approach.

Odum, E. P. 1953. Fundamentals of Ecology. Saunders, Philadelphia, PA, 384 pages.

A classic textbook of ecosystem ecology. The book fully embraced the ecosystem approach and was a standard ecology text for several decades with the latest reprint appear as Odum, E.P. and Barret, G.W. (2005). Fundamentals of Ecology, 5th Ed., Belmont, CA, Thompson Books/ole. 598 pages.

Schlesinger, W.H. and E.S. Bernhardt. 2013. *Biogeochemistry: An Analysis of Global Change*. 3rd edition. Academic Press/Elsevier, New York. 664pp.

A comprehensive and contemporary treatment of the field of biogeochemistry. The book provides descriptive information on structure and regulation of biogeochemical cycles and the consequences of human activity on them.

R. W. Sterner and J. J. Elser (2002) Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton University Press. pp.584.

An important text on ecological stoichiometry – the study of the effects of the relationship between energy and elements affects and is affected interactions and processes in ecosystems.

Ecosystem Processes – Human Impacts

There are numerous papers, books, and reports that cover specific biogeochemical cycles and the environmental consequences of altering them. Carpenter et al. (1998) and Schindler and Vallentyne (2004) provide excellent reviews of the sources and consequences of nutrient loading

– eutrophication- to freshwater systems. Dybas (2005) covers the growing concern over the hypoxic areas in marine and large lake systems known as dead zones, caused by nutrient pollution. Baron et al. (2013) summarizes several studies on the regional effects of anthropogenic reactive nitrogen and climate change on aquatic systems. Caldeira and Wickett (2003) provide a detailed accounting of the extent of and effect of elevated atmospheric CO_2 concentrations on ocean pH. The working groups of the Fourth assessment Report of the UN Intergovernmental panel on climate change (IPCC 2007) produced three reports and a synthesis report on the consequences of greenhouse gases on ecosystems structure and function along with a series of mitigation and adaptation strategies.

Baron, J. S., E. K. Hall, B. T. Nolan, J. C. Finlay, E. S. Bernhardt, J. A. Harrison, F. Chan, and E. W. Boyer. 2013. The interactive effects of excess reactive nitrogen and climate change on aquatic ecosystems and water resources of the United States. Biogeochemistry 114:71–92.

An excellent review of how human activity has enhanced reactive nitrogen interacts with changes in patterns of precipitation to affect biogeochemical cycles and aquatic ecosystems.

Caldeira, K., and Wickett, M.E. (2003). Anthropogenic carbon and ocean pH. Nature 425: 365–365.

The paper details the consequences of elevated CO_2 on ocean pH.

Carpenter, S.R., Caraco, N.F., Correll D.L., Howarth, R.W., Sharpley, A,N. Smith, V.H. (1998). Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications*. **8** (3): 559–568.

The paper provides an excellent review of sources and the consequences of nonpoint sources of phosphorous and nitrogen on surface waters. The authors provide a series of recommendations to reduce these sources.

Dybas, C.L. (2005). Dead Zones Spreading in World Oceans. *BioScience*. **55** (7): 552–557

An excellent account of the formation and extent of dead zones in ocean systems.

Academy of Science 50: 221–246.

Formalizes the importance of biochemical cycles to ecosystems by making a distinction between *biochemical* approach and the flow of matter among organisms and the *biodemographic* approach and population dynamics of organisms.

Schindler, D. and Vallentyne, J.R. (2004) Over fertilization of the World's Freshwaters and Estuaries, University of Alberta Press

An excellent resource and review of nutrient loading on freshwater systems.

Contribution of Working Groups, I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (2007). Climate Change 2007: Synthesis Report. Parry, M.L., O.F. Canziani, O.F., Palutikof, J.P., van der Linden, P.J., and Hanson, C.E., Eds. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

The summary report to the fourth assessment report Intergovernmental Panel on Climate Change. A concise read on the findings of working groups I, II, and III. The report makes the connection between human activity and climate change and proposes a series of mitigation and adaptation strategies.

Ecosystem Services

Ecosystem services represent the benefits that people obtain from ecosystems (Millennial Ecosystem Assessment, MEA 2005). The concept formalizes how aspects of ecosystem structure, function and dynamics affect human well-being and is central to the conceptual framework of the Millennium Ecosystem Assessment (2005). Per the MEA framework, ecosystem services include foundational supporting services (e.g., primary production, nutrient cycling, evolution, spatial structure, and soil formation), provisioning services (e.g., food, water, fiber, fuel, biochemical, genetic resources), regulating (e.g., climate regulation, water regulation, water purification, pollination, and disease), and cultural services (e.g., spiritual and religious, recreation, ecotourism, cultural heritage, aesthetic, recreation, and education).

Millennial Ecosystem Assessment (2005). Ecosystems and Human Well-being Synthesis. World Resources Institute, Washington, DC.

Series of reports developed to catalogue the state of the world ecosystems and to establish the scientific basis for action to sustain ecosystems and the contributions they make for human well-being.

History of Ecosystem Ecology

Ecosystem ecology is a relatively young discipline. Golley (1993) and Coleman (2010) provide excellent reviews of the history of ecosystem science and first-hand accounts of the fields development. Elements of the foundations of the science go back centuries, but began to coalesce in the late 19th Century and early 20th Century. During the early part of the 20th Century, there is a rapid shift in what was considered traditional ecology to what is now recognized as modern ecosystem thinking. The field was formalized in the late 20th century after World War II. Contemporary ecosystem thought has further evolved and the field now embraces the importance of social and human dimensions. Golley (1993) focuses on the historical development of the field in general, but prior to the establishment and development of the social-ecological perspective. Coleman (2010) traces the development of the field by focusing on the large international and national initiatives that were took hold in response to the International Geophysical Year (1957-1958).

Coleman, D.C. 2010. Big Ecology: The emergence of Ecosystem Science. University of California Press, Berkeley, CA.

An easy to read accounting of the developments that place in ecosystem ecology during the later half of the 20th century. The book is written from a participant's perspective providing insights into the advances in ecosystem science and the large-scale initiatives that were undertaken.

Golley, F.B. (1993). A History of the Ecosystem Concept in Ecology. Yale University Press, New Haven, Connecticut.

An interesting and thorough description of the history of the ecosystem concept as it developed during the 20th century.

Foundational Works

Tansley (1935) first published the term *ecosystem*, defined as the fundamental units of nature formed by the coupling of the interactions among organisms and the physical factors within the environment. The ecosystem concept can be traced back to Möbius (1877) and the idea of biocoenosis of communities, the work of Clements (1916) on plant succession, and the contributions of Elton (1927) on community development and structure. Möbius coined the term *biocoensis* to represent a description of the interactions among organisms living in a specific habitat or *biotope*. Clements took this view a step further by viewing mature communities as entities in and among themselves, possessing the capacity to reproduce it parts and the ecological succession leading to their development as a form of ontogeny akin to the developmental stages of an individual species. Elton applied the law of thermodynamics to ecological systems leading to the modern concept of a food chain and food web, defining them not only in terms of the species that were present but of the matter and energy contained within, as illustrated in his concepts of the pyramids of numbers and biomass, respectively. Tansley's definition in essence melded the concepts of *biocoensis* and *biotope*, and the idea that ecosystems were natural entities shaped by Eltonian principles rather than the Clementian notion of the 'super-organism' organization and development.

Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Carnegie Institute of Washington Publication 242. Washington, D.C.: Carnegie Institution of Washington.

Foundational publication wherein Clements defines a community as a superorganism and the process of succession and community development as a deterministic process that leads to a climax community. The ideas that are presented are dated, but provide an important context from which the ecosystem perspective emerged.

Möbius, Karl 1877. *Die Auster und die Austernwirtschaft.* Verlag von Wiegandt, Hemple & Parey: Berlin.

Introduces the concept of biocoenesis or the biological community – organisms living together in a defined habitat. The English translation - The Oyster and Oyster Farming – is available in the *U.S. Commission Fish and Fisheries Report*, 1880: 683-7510.

Tansley, A. G. (1935). The use and abuse of vegetational terms and concepts. *Ecology* **16** (3): 284–307. doi:10.2307/1930070

The paper that provides the first modern definition on the ecosystem. Tansley stresses that the ecosystem consists of both living and non-living (organic and inorganic) components. The ecosystem is presented as a fundamental concept of nature wherein organisms and inorganic components exist in a "…relatively stable dynamic equilibrium."

Development of Modern Ecosystem Thinking

Slobodkin (1993) credits the ecologist G. Evelyn Hutchinson as having had a major impact on the development of ecology the through his work and that of his students by transforming ecology from a description science to a predictive science. Hutchinson championed the use of mathematics and quantifying observations to answer basic questions and test hypotheses. He balanced the need to understand organisms in the ways that early naturalists studied them, with the holistic approach that included biogeochemical cycling, and exchanges with the geophysical world typically studied in earth systems science (Hutchinson 1948). His work on energy flow and the cycling of phosphorus in lakes and the use of isotopes to study nutrient dynamics and energy flow pioneered the field (Hutchinson 1941). Lindeman (1942), a student of Hutchinson, published a seminal paper that epitomizes this new synthesis and perspective by representing the ecosystems in terms of species interactions in the context of the abiotic environment and by quantifying not only the biomasses of the species but by the flows among species. His description of the food web of the Cedar Creek Bog defined groups of species interactions in energetic terms, and included detritus (Ooze), microbes, and nutrients, as direct inflows and outflows in ways that encapsulated the ecosystem concept and ecosystem practice.

Hutchinson, G.E. (1959). Homage to Santa Rosalia, or why are there so many finds of animals. The American Naturalist **93**:145-159.

A published version of this address to the Society of the American Naturalists wherein a variety of then contemporary issues in ecology were...

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399-418.

A seminal paper in ecosystem ecology that proposes an energetics view of ecological interactions. The work is empirically-based and theoretical, providing a detailed description of a system to convey abstract ideas. The work is one of the first to integrate living and dead organic material, being one of the first to explicitly include detritus – ‘ooze’.

Slobodkin, L. B. (1993). An appreciation: George Evelyn Hutchinson. Journal of Animal Ecology. **62** (2): 390-394.

A tribute to the life of G. Evelyn Hutchinson written by a former student. The paper provides a summary of not only the contributions that Hutchinson made to the field of ecology, and the ecosystem concept, but important developments in thinking that were taking place as well.

Formalizing Ecosystem Ecology as a Discipline

In 1953, Eugene P. Odum with the help of his brother Howard T. Odum (a student of Hutchinson) published one of the first textbooks in ecology – *Fundamentals of Ecology* (first edition). The approach presented, formalized a holistic approach to studying organisms in their environment, drawing on natural history, earth system science and ecological energetics (i.e., study of energy flow). The book represents a departure from previous works and marked a beginning of the formalization of the ecosystem approach in ecology, and ecology as a discipline. The ecosystem approach was well aligned and suited to address the scope and vision of several large international and national initiatives emerged from the International Geophysical Year (1957-1958) (discussed below). Odum (1969) presented the *Strategy of Ecosystem Development*, wherein characteristics of ecosystems during their developmental and mature stages were compared. The ideas are more phenomenological than explanatory, in that they do not ascribe explicit mechanisms. The paper takes a holistic approach by positioning the ecosystem, not the species that comprise it, at the center of the discussion. While a contemporary set of ideas from the community-based ecology approach in *Theory of Island Biogeography* presented by MacArthur and Wilson (1967) explained observed patterns of species diversity based on differential rates of colonization and extinction, the mechanisms that lead to the changes underlying the contrasts between the developing and mature communities are not clearly spelled out, but unlike it, does not assume that process operate in an equal manner at random on species or other components of the system. In the *Strategy of Ecosystem Development*, Odum (1969) embraces the co-evolution between species and feedbacks between organisms and abiotic factors (inorganic nutrients), to bring an ecosystem and its components and processes in balance. The ecosystem possessed cybernetic properties engrained in the genetic make-up of the constituent species and governed by the first and second laws of thermodynamics and the conservation of matter.

MacArthur, R. M., and Wilson, E.O. (1967). The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

An outstanding example of the power of the scientific method and how theory emerges from years of empirical observation and experimentation.

Odum, E. P. 1953. Fundamentals of Ecology. Saunders, Philadelphia, PA, 384 pages.

A classic textbook of ecosystem ecology. The book fully embraced the ecosystem approach and was a standard ecology text for several decades with the latest reprint appear as Odum, E.P. and Barret, G.W. (2005). Fundamentals of Ecology, 5th Ed., Belmont, CA, Thompson Books/ole. 598 pages.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-279.

A summary of ecosystem structural, functional and dynamic properties for early and late successional properties. Odum offers the comparison as a basis for general ecosystem science theory.

Contemporary Views – Theory and Practice

Ecosystem ecology has undergone major transformations over the past couple of decades. The theoretical basis of the science and how it is practiced has been consistently challenged both from within and from outside the community. O'Neill (2001) delivered a poignant address upon receiving the MacArthur Award at the annual meeting of the Ecological Society of America in 2000. He appears to have challenge basic tenets of ecosystem science altogether, citing the lack of a coherent theoretical under-pinning. This seeming rebuke was more of a pivot away from the cybernetics leanings of earlier thinking to more of a principle-based approach. This address had been preceded by several calls to invoke theory in ecosystem studies if not ecology writ large (Levin 1989). Carpenter (1998) advocated use of observations in space and time, experiments and theory, the later being conspicuously absent or given short shrift. The debate is ongoing.

Knapp and D’Avanzo (2010) provide a review of principles that form the basis ecosystem ecology from a teaching perspective. In a special issue commemorating the 20-year anniversary of the establishment of the journal *Ecosystems*, Cottingham et al. (2017) revisit this debate, reminding the field that theory needs to be the foundation of ecosystem ecology.

Carpenter SR. 1998. The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. In: Pace ML, Groffman PM, Eds. Successes, limitations, and frontiers in ecosystem science. New York: Springer. p 287–312.

The author makes the case for large scale experiments that use multiple lines of inference are necessary to understand how ecosystems function to study ecosystem responses to disturbance. The metaphor of a table with legs representing theory, observations in space, observations in time, and experiments is used to represent the multiple lines of inference.

Cottingham, K.L., Fey, S.B., Fritschie, K.J., and Trout-Haney, J.V. 2017. Advancing ecosystem science by promoting greater use of theory and multiple research approaches in graduate education. Ecosystems On-line, DOI: 10.1007/s10021-016-0070-3

A well-written account and review of the role of theory in shaping ecosystem science, and the different modalities of practice within the field. The authors stress the need to integrate theory in practice.

Knapp, A.K. and D’Avanzo, C. (2010). Teaching with principles: toward more effective pedagogy in ecology. Ecosphere 1:1–10 DOI: 10.1890/ES10-00013.1

An excellent paper that reviews key ecological principles and aligns them with innovative instructional strategies.

Levin S.A. 1989. Challenges in the development of a theory of community and ecosystem structure and function. In: Roughgarden, J., May, R.M., Levin, S.A., Eds. Perspectives in ecological theory. Princeton (NJ): Princeton University Press. p 242–55.

This paper reviews mathematical models that are used to study environmental disturbance on ecosystem processes such as productivity, nutrient cycling, and succession. The author addresses the need to couple biological and physical factors and components that are operating on different spatial and temporal scales.

O'Neill, R. V. 2001. Is it time to bury the ecosystem concept? (With full military honors, of course!). Ecology 82:3275-3284.

The paper was a summary of O'Neill's address to the Ecological Society of America for hi receiving the Robert MacArthur award. The paper is an honest assessment of the state of ecosystem science at the end of the 20th Century. O'Neill offers a series of tenets that could strengthen the field.

Contemporary Views - Social and Human Dimensions

Ecosystem ecology has evolved as a discipline to include human interactions and now serves as a foundational discipline for the modern development of urban ecology, elements of landscape ecology (Clark 2010), and sustainability science. The discipline has long influenced natural resource management and agriculture adopted as practitioners have adopted basic ecosystem principles into the management of forest, rangeland and agricultural settings. The major evolution to the science has been in how humans and their actions are positioned within the discipline, as the epistemological perspective of the social sciences worked its way into ecosystem ecology. Early studies either studied ecological interactions in urban centers or human dominated landscapes or explicitly incorporated humans into studies much like any other organism. Pelt (1977) advocated fundamental changes in the relationship between humans and urban centers that incorporated ecological principles to better human well-being. Coughenour et al. (1985) presented an analysis of the energy flows within an arid tropical ecosystem that included the Ngisonyoka pastoralists in the Turkana region of Kenya as being an integral component of the system. The study presented one of the first detailed accounts of human energy utilization from an ecosystem perspective; the key feature was that humans were treated as other organisms engaged in trophic interactions, responding to environmental conditions and affecting the local environment. The system was described as being maintenance rather than production oriented, with the energy utilization of Ngisonyoka being "…consistent with the ecological patterns that promote rather than diminish stability under stress." Other approaches catalogued the impacts of humans on ecosystem structure and function. Vitousek et al. (1997) presented the lead paper in a Special Issue in the journal *Science* entitled Human-Dominated Ecosystems that cataloged the extent to which humans affect ecosystem structure and function on a global scale. Humans have affected ecosystems and ecosystem processes to the point that the idea that natural ecosystem – those without human influence - exist should be challenged and questioned what future ecosystem states might be (Matson et al. 1997). These papers represent the forbearers to a shift in the science to formally include a social or human dimension (read social-ecological perspective, Pickett et al. 1997, Collins et al. 2010) to the point that ecosystem ecology and the services that ecosystems provide (Millennium Ecosystem Assessment 2005) now forms basis of modern sustainability science, as it represents the ecology and environment in the triple bottom line of ecology, economy, and social of sustainability, and provides the systems approach to study the complexity of sustainability.

Collins, S.L., Carpenter, S. R., Swinton, S.M., Orenstein, D.E., Childers, D.L., Gragson, T.L., Grimm, N.B., Grove, J.M., Harlan, S.L., Jason P Kaye, J.P., Knapp, A.K., Kofinas, G.P., Magnuson, J.J., McDowell, W.H., Melack, J.M., Ogden, L.A., Robertson, G.P., Smith, M.D., and Whitmer, A.C. 2010. A conceptual framework for long-term social-ecological research. The "Press-Pulse Dynamics" concept is used to integrate the biophysical and social sciences. Frontiers of Ecology and the Environment 9(6):351-357.

The paper advocates the use of the Press-Pulse Dynamics concepts from ecosystem ecology as a framework to study social-ecological systems.

Clark, W.R. 2010. Principles of landscape ecology. Nature Education Knowledge 3:34

A overview of the development of landscape ecology and its theoretical underpinnings.

Coughenour, M.B., Ellis, J.E., Swift, D.M., Coppock, D.L., Galvin, K., McCabe, and Hart, T.C. (1985). Energy extraction and use in a nomadic pastoral ecosystem. Science **230**: 619-625.

An excellent application of the ecosystem perspective to a human population and its interactions with the environment.

Matson, P.A., Parton, W.J., Power, A.G., and Swift, M.J. (1997). Agricultural intensification and ecosystem properties. Science **277**, 504-509.

The paper documents the extent of agricultural intensification and its impact on biotic interactions and resource allocation. The authors advocate the adoption of ecologically based management strategies.

Millennium Ecosystem Assessment (MA). 2005. Ecosystems and Human Well-Being: Synthesis. Island Press, Washington. 155pp.

One of a series of volumes produced as part if the Millennium Ecosystem Assessment. This volume defines and summarizes the concept of Ecosystem Services. This volume and the companion volumes are excellent resources.

Pelt, J.M. (1977). The re-naturalized Human (French: L'homme re-naturé) (1977), Eds. Le Seuil. ISBN 2-02-004589-3

The paper presents a re-thinking of the relationship between humans and urban centers. Largely viewed as a precursor to modern urban ecology.

Pickett, S.T.A., Burch, W.R. Jr., Dalton, S.E., Foresman, T.W., Grove, J.M., and Rowntree, R.A. (1997). A conceptual framework for the study of human ecosystems in urban areas. Urban Ecosystems 1:185-199.

The paper proposes a framework for studying the role of humans in ecosystems. The authors stress that the ecosystem concept can serve as the basis, but that specific social attributes of humans and their institutions such as learning must be added.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., and Melillo, J.M. (1997). Human domination of Earth's Ecosystems. Science **277**, 494-499.

A comprehensive synthesis of the impact that humans are having on the Earth's ecosystems. The paper represents an important tipping point in thinking by clearing showing the global extent of human impacts.

Systems Theory and Information Theory

Ecosystem ecology has been heavily influenced by the ideas that emerged from information theory, hierarchy theory, cybernetics, and complexity theory (Tansley 1935, Simon 1962, Odum 1969, Allen and Starr 1982, Waldroff 1992). Tansley rejected the extreme nature of the superorganism concept pushed by Clements (discussed above), but embraced the hierarchical systems thinking that it embodied. In fact, in defining the ecosystem, Tansley (1935) referred them as forming *"… one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom."* Hutchinson (1948) and other ecologists of the time became interested in the field of Cybernetics - the science of control and communication. The term Cybernetics was coined from the Greek word "kubernetes", meaning steersman or governor, from the radical "kuberman", meaning to steer or govern. The concept relies on the flow of information among constituents to control processes within an organized system, and on the notion that the system is in homeostasis or strives toward it. The ideas presented by Odum (1969) generated intense debates over the entire concept of the ecosystem and their purported cybernetic properties. McNaughton and Coughenour (1981) made the case that an ecosystem was a cybernetic system in that they possessed coordination, regulation, communication, and control through the information flow embedded in trophic interactions (*sensu* Lindeman 1942, and Hairston *et al*. 1960) among species and their interactions with the abiotic environment. While elements of cybernetic organization are apparent, O'Neill *et al.* (1986) make a poignant case that the concept is incomplete in that it relies on homeostasis and does a poor job in explaining the reaction of systems to stress and instability. Ecosystems might possess cybernetic properties but the concept does not represent the fundament organizing principle that shapes and guides them. In its place, O'Neill *et al.* (1986) apply the concept of hierarchical organization to ecosystems. Parallel to these developments was the advance of complexity science and the concept of the complex adaptive system (Waldrop 1992, Levins 1998). Complex adaptive systems possess hierarchical organization of subsystems of self-similar interacting components, possess the capacity to adapt and evolve (read co-evolve with its environment), and shun the notion of homeostasis as they often operate far from equilibrium conditions. While not fully accepted by the community, the perspectives embodied in complex adaptive thinking provide a means of advancing ecosystem ecology, particularly when the social and human dimensions are considered.

Allen, T.F.H., and Starr, T.B. (1982). Hierarchy Theory: Perspectives for Ecological Complexity. University of Chicago Press, Chicago.

The book presents the basic concepts of hierarchical organization and connections between structure, function, and dynamics as they relate to ecological systems. The importance of temporal and spatial scales and their relationships of structure to function and dynamics are discussed.

Hairston, N.G., Smith, F.E., and Slobodkin, L.B. (1960). Community structure, population control and distribution. The American Naturalist, 94, 89-98.

A classic paper that addresses the many concepts of the relationships among community structure, functional aspects of ecosystems and their dynamics. In many ways this a a companion read to Hutchinson (1959) listed above.

Hutchinson, G.E. (1948). Circular Causal Systems in Ecology. Annals of the New York Academy of Sciences 50:221-246.

An important paper that lays out the framework for what became the model ecosystem approach.

Levin, S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. Ecosystems 1:43136.

The paper makes a strong argument and case that ecosystems and the biosphere are best described as and studied as complex adaptive systems.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-279.

A summary of ecosystem structural, functional and dynamic properties for early and late successional properties. Odum offers the comparison as a basis for general ecosystem science theory.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B., and Allen, T.F.H. (1986). A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, N.J., 253 Pages.

An excellent presentation and argument to define the ecosystem concept based on the tenets of hierarchy theory.

Simon, H.A. (1962). The architecture of complexity. Proceeding of the American Philosophical Society, 106:467-482.

A lengthy but interesting read on the nature of complex systems. The paper lays the foundation for hierarchy theory.

Waldrop, M.M. (1992). Complexity: the Emerging Science at the Edge of Order and Chaos. New York: Touchstone.

The book covers the fundamentals of complexity and complex adaptive systems.

Ecosystem Models

Ecosystem ecology has embraced models and mathematics as a means to develop and test theory, to integrate multiple components, to catalog interactions, and to generate predictions. The development of the field coincided with advances in information theory and modern computing. May (1973) categorized models used in ecology as being arranged along a continuum bounded by purely strategic models designed to test general theory and tactical models designed to describe phenomena (read ecosystem processes) or system in detail. The models used in ecosystem ecology spanned this continuum have embracing both modeling strategies, but tended early on to follow the tactical mode using energetic and biogeochemical approaches. The earliest representations can be traced predator prey systems based on differential equations designed to study their dynamics, and food chains and food webs designed to illustrate the cycling of matter (Lotka 1927, Elton 1927). Currencies used to parameterize the models include population sizes and biomass. Lindeman (1942) provided a comprehensive description of the ecosystem in energetic terms that established a new framework to study systems that formalized the study of energy and material flow (see Odum 1953), and introduced the concept of the trophic level. MacArthur (1955) and DeAngelis (1975) melded traditional equation based models to the concepts of energy flow to study food web dynamics (see Moore and de Ruiter 2012 for an overview). Parton et al. (1987) developed a general process oriented model – Century – to describe the cycling of soil organic matter in terrestrial systems (see also Parton et al. 2015). These approaches are used extensively to study ecosystems and ecosystem processes, often used with or to develop elements of spatial models of and climate models, over a range of spatial and temporal scales (Rastetter et al. 2003).

Elton, C.S. (1927). Animal Ecology, Republished in 2001, University of Chicago Press, Chicago IL.

This classic text provides the foundation of many general ecological and ecosystem concepts.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36 (3): 533-536.

An early treatment of the relationship between population dynamics and stability. The concepts of community organization as multiple pathways of trophic interactions and redundancy of pathways to are presented.

May, R.M. 1973. Stability and Complexity of Model Ecosystems. Princeton University Press, Princeton, N.J.

The covers fundamental approaches to modeling ecosystems. The book is clearly written and provides a solid foundation on the use differential and difference equations to model simple ecological communities.

Moore, J.C. and de Ruiter, P.C. (2012). Energetic food webs: Ana analysis of real and model ecosystems. Oxford University Press, Oxford, UK.

The book uses both the community-based and ecosystem-based approaches to study the relationship between food webs structure, biogeochemistry (functional aspects) and dynamics.

Parton, W.J., Schimel, D.S., Cole, C.V., and Ojima, D.S. (1987). Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51:1173-1179.

An early description of the CENTURY model and its application. This is one of the most widely used models to study soil organic matter dynamics. A number of variants of the model has since been developed (see Parton et al. 2015)

Parton W.J., S.J. Del Grosso, A.F. Plante, E.C. Adair, and S.M. Lutz. 2015. "Modeling the dynamics of soil organic matter and nutrient cycling." In Soil microbiology, ecology and biochemistry. 4th ed. Edited by Paul, E.A., pp. 505-538. San Diego, CA: Academic Press.

This chapter provides and overview of soil organic matter models.

Rastetter, E.B., Aber, J.D., Peters, D.P.C., Ojima, D.S., and Burke, I. 2003. Using mechanistic models to scale ecological processes across space and time. BioScience 53: 68-76.

Explores the value of using models and empirical data collected over different temporal and spatial scales to understand ecosystem process across space and time. The paper is part of a special feature on the US Long Term Ecological Research (LTER) Network.

Large Initiatives

The ecosystem perspective has served as the basis for several large national and international initiatives (Aronova 2010, Coleman 2010). International Geophysical Year (1957-1958) provided the impetus for a new way of conducting ecological science – collaborative big data driven science. The ecosystem approach seemed well suited to lead these efforts. A partial listing of the programs within the US includes the International Geophysical Year (IGY: 1957-1958), The International Biological Program (IBP: 1964-1974), the US Long Term Ecological Research Program (LTER 1980-present), and the National Ecological Observatory Network (NEON: 2008-present). These large initiatives have had a profound effect on the development of ecosystem ecology and reflect the development, challenges and benefits of ecosystem ecology. Coleman (2010) provides an overview of the history of these initiatives in his book *Big Ecology – The emergence of ecosystem science*, while Aronova et al. (2010) provides an overview of the impact of these program on science writ large. C.H (1975) provided a synopsis of a report by the National Academy of Sciences on the IBP, the findings of which were mixed. Among participants, the report cited that the IBP '…validated the interdisciplinary team approach to the study of ecosystems as well as the use of systems analysis and mathematical modeling, which they say, has turned ecology from a descriptive science into one with predictive capabilities that will aid policy-makers in making sophisticated decisions on resource management.' Among nonparticipants, the report noted that many felt that '…the biome studies have accumulated masses of data while failing to establish chains of cause and effect that could lead to deeper understanding of how ecosystems work.' Boffey (1976) questioned the cost of the IBP. Hobbie (2003) provides the lead paper in a special issue of *BioScience* that highlights the science of the NSF LTER program. The long term perspective and the distributed nature of the sites within diverse regions and biomes has produced a significant advance in ecosystem ecology, particularly in our understanding of how ecosystems processes respond to change at different locations and at different spatial scale, and of how processes that operate over decadal time steps may drive or interact with local conditions. Mervis (2015) provides a critical assessment of the development and launch of the NEON network – '…a continental-scale observatory that would monitor environmental change into a concrete plan.'

Aronova, E., Baker K.S., Oreskes, N. 2010. Big science and big data in biology: From the International Geophysical Year through the International Biological Program to the Long Term Ecological Research (LTER) Network, 1957-present. *Historical Studies in Natural Science* 40(2): 183-224.

The paper follows the development of ecosystem ecology in the era of big science and bid data; defined as the synoptic collection of observational data on a global geographic scale.

Boffey, P.M. 1976. International Biological Program: Was It Worth the Cost and Effort? Science 193: 866–68.

A critical assessment of the international biological program.

C.H., National Academy of Sciences (1975) "NAS Report on International Biological Program," Science 187: 663.

A candid assessment of the successes and perceived failure of the International Biological Program.

Coleman, D.C. 2010. Big Ecology: The emergence of Ecosystem Science. University of California Press, Berkeley, CA.

An easy to read accounting of the developments that place in ecosystem ecology during the later half of the 20th century. The book is written from a participant's perspective providing insights into the advances in ecosystem science and the large-scale initiatives that were undertaken.

Hobbie, J.E., Carpenter, S.R., Grimm, N.B., Gosz, J.R., and Seastedt, T.R. (2000). Scientific accomplishments of the Long Term Ecological Research Program: An introduction. BioScience 53: 21–32.

Lead paper of a special issue of *BioScience* that highlights the rational and importance of the NSF Long Term Ecological Research Program. The companion papers touch on many of the aspects of ecosystem ecology discussed above.

Mervis, J. (2015). Ecology's tough climb. Science 349: 1436-1441.

A candid assessment of the launch of the National Ecological Observatory Network.