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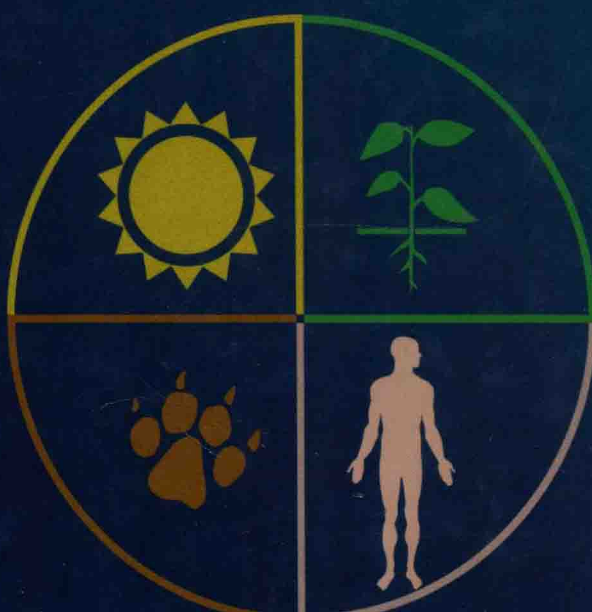

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ECOSYSTEM ECOLOGY

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PREFACE

Systems ecology, also called ecosystem theory, offers today a complete theory about how ecosystems are working as systems. The theory will inevitably be improved in the coming years, when it hopefully will be used increasingly to explain ecological observations and to facilitate environmental management including the use of ecotechnology. The theory is, however, sufficiently developed today to be presented as a complete theory that offers a wide spectrum of applications. Only through a wider application of the theory – or let us call what we have today propositions of a theory – it will be possible to see the shortcomings of the present theory and propose improvement of the theory.

The book consists of three parts. The part Ecosystems as Systems emphasizes the system properties of ecosystems including the presentation of basic scientific propositions to a theory in the chapter Fundamental Laws in Ecology, while the part Ecosystem Properties gives a more comprehensive overview of the holistic properties of ecosystems, which of course – not surprisingly – are rooted in the system properties and covered by the propositions. The part Ecosystems gives an overview of different types of ecosystems, how they function due to their characteristic ecosystem properties, and how the scientific propositions can be applied to understand and illustrate their characteristic properties.

It is my hope that this book will be utilized intensively by ecologists and system ecologists to gain a deeper understanding of ecosystems and their function and to initiate the development of ecology toward a more theoretical science that can explain and predict reactions of ecosystems. By such a development, it will be possible to replace many measurements that are often expensive to perform with sound theoretical considerations.

The book is based on the presentation of

I. systems ecology as an ecological subdiscipline and
II. a very comprehensive overview of all types of ecosystems with many illustrations of their characteristic properties

in the recently published *Encyclopedia of Ecology*.

Due to an excellent work by the editor of the Ecosystem Section, Donald de Angelis, and the editor of the Systems Ecology Section, Brian Fath, in the *Encyclopedia of Ecology*, it has been possible to present a comprehensive and very informative overview of all types of ecosystems and an updated ecosystem theory. I would therefore like to thank Donald and all the authors of ecosystem entries and Brian Fath and all the authors of systems ecology entries for their contributions to the *Encyclopedia of Ecology*, which made it possible to produce this broad and up-to-date coverage of a very important subdiscipline in ecology.

Sven Erik Jørgensen
Copenhagen, May 2009

CONTENTS

ECOSYSTEMS AS SYSTEMS

Introduction

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According to the definition by Tansley (1935), an ecosystem is an integrated system composed of interacting biotic and abiotic components. It is important in this definition that an ecosystem is a system, which implies that it has boundaries and that we can distinguish between the system and its environment – environment in principle means the rest of the world beyond the boundaries of the system. The components – biotic as well as abiotic – are interacting, which means that they are connected directly or indirectly. All systems that encompass interacting biotic and abiotic components may be considered as an ecosystem. A drop of polluted water may for instance be considered an ecosystem, because it contains microorganisms, organic matter, and inorganic salts and these components are interacting. Usually, our ecosystem research and management is interested in a larger area of nature characterized by its function and properties, for instance a lake, a forest, or a wetland. All these three examples of ecosystems have very characteristic functions and have several unique properties that are different from other types of ecosystems. The scale that is applied for the definition of an ecosystem is dependent on the function of the ecosystem and is determined by the addressed problem.

Because an ecosystem has interacting and connected biotic and abiotic components, it has system properties in the sense that the components work together to give the system emerging properties and make the system more than just the sum of the components. A living organism is much more than the cells and the organs that make up the organism. Similarly, a forest is more than just the trees – it is a cooperative working unit with emerging unique properties characteristic of a forest.

It is important to understand fully the function and the reactions of ecosystems in both ecological research and environmental management. The two basic questions in this context are

1. Which fundamental properties characterize ecosystems?
2. Is it possible to formulate basic scientific propositions that are able to explain the functions of ecosystems?

It is attempted to answer these two core questions in the parts Ecosystems as Systems and Ecosystem Properties of this book, while the part Ecosystems gives an overview of different types of ecosystems, how they function due to their characteristic ecosystem properties, and how the scientific propositions can be applied to understand and illustrate their characteristic properties. The part Ecosystems as Systems emphasizes the system properties of ecosystems and also presents basic scientific propositions, while the part Ecosystem Properties gives a more comprehensive overview of the holistic properties of ecosystems, which of course – not surprisingly – are rooted in the system properties.

The chapters Ecosystem Ecology, Ecological System Thinking, and Ecosystems in the part Ecosystems as Systems focus on the most fundamental system properties that are derived from the above-presented definition of ecosystems. The definition is repeated in all three chapters with slight modifications. The system properties presented in these three chapters may be summarized as follows:

1. Ecosystems cycle energy.
2. Ecosystems cycle matter.
3. Life and environment are connected, which implies that the environment of an ecosystem influences the ecosystem. This influence determines the prevailing conditions of the ecosystems, or expressed differently the external variables (also called forcing functions) determine the conditions for the internal variables (also called state variables) of an ecosystem. The wide spectrum of different ecosystems (the part Ecosystems gives an overview) is the result of an overwhelmingly large number of different conditions (combinations of external variables).
4. Ecosystems are whole systems and studies of ecosystem dynamics therefore require holistic views.

The human society is very dependent on the proper functioning of ecosystems, because humans are using a wide spectrum of services offered by the ecosystems. It is therefore important to understand the ecosystem properties on which these services are based. The chapter Ecosystem Services and partly the chapter Ecosystems present the ecosystem services, which may be classified into three groups:

- production services as we know them from agriculture, fishery, forestry, and so on;
- regulation services due to cycling, filtration, translocation, and stabilization processes;
- cultural services such as recreation, spiritual inspiration, and esthetic beauty.

The chapter Fundamental Laws in Ecology gives a brief summary of the ecosystem properties that are rooted in the system properties of ecosystems:

- Ecosystems are complex (many steadily varying interacting components).
- Ecosystems are open.
- Ecosystems are hierarchically organized.
- Ecosystems are self-organizing and self-regulated due to a very large number of feedback mechanisms.

These properties are discussed in more detail in the part Ecosystem Properties.

The chapter Fundamental Laws in Ecology proposes 10 fundamental laws of ecosystems that are consistent with the system properties presented in the other chapters of the part Ecosystems as Systems. The 10 propositions are able to explain ecosystem behavior and properties. The fundamental tentative laws presented in this chapter are furthermore able to explain many ecological observations and rules, which is a great advantage of having a good theory. By use of the theory, it is possible to conclude, without the need for observations, how an ecosystem will react to different impacts. It is therefore indeed possible to improve research plans and develop environmental management plans on the basis of theoretical considerations. The 10 propositions (tentative laws) can be shown to be rooted in five basic ecological system properties.

The part Ecosystem Properties gives more information on the basic properties of an ecosystem. The chapter Autocatalysis focuses on autocatalysis, which frequently increases the efficiencies and rates of ecological processes. The chapter Body Size Patterns discusses the body size pattern of ecosystems. The rate of biological processes such as growth, metabolism, mortality, generation time, and respiration is dependent on the size of the organisms. The spectrum of conditions in an ecosystem determines the spectrum of these fundamental ecological processes, which would allow the best utilization of the resources in ecosystems. It implies that the conditions also determine the body size pattern. Different ecosystems at different conditions may therefore have a different body size pattern, which therefore becomes a characteristic property of an ecosystem.

All ecosystems cycle the elements that are essential for the living matter, and thereby the growth and development of ecosystems can continue, because the essential elements are steadily recovered with a certain rate. The living matter needs about 22 different elements, of which the cycling of nitrogen, carbon, phosphorus, sulfur, silica, calcium, sodium, and magnesium is of utmost importance. The cycling is possible due to the ecological networks that are formed in all ecosystems. The network may be considered a 'map' of the connections of abiotic and biotic components. The network indicates the possibilities for interactions among the components of the ecosystem. Obviously, cycling is very important for ecosystems, because without cycling the growth and development of biological components would stop due to the lack of one or more essential elements. The chapter Cycling and Cycling Indices covers cycling and cycling indices, which quantify the network's possibilities to support the cycling processes.

The chapters Ecological Network Analysis, Ascendancy; Ecological Network Analysis, Energy Analysis; Ecological Network Analysis, Environ Analysis; and Indirect Effects in Ecology present different aspects of the ecological network. Network analysis, ENA (Ecological Network Analysis), uses network theory to study the interactions between organisms or populations within their environment. Ascendancy, which is covered in the chapter Ecological Network Analysis, Ascendancy, quantifies the efficiency of the networks on the basis of the actual flows. Development of an ecosystem will usually imply that the ascendancy is increasing. The chapter Ecological Network Analysis, Energy Analysis analyzes the ecological network by use of the energy flows, while the chapter Indirect Effects in Ecology uses the so-called environ analysis. Each object in the system has two 'environs', one receiving and one generating interactions in the system. It is by analyzing these flows that it is possible to deduce network properties such as network mutualism and network synergy. Cycling – the topic of the chapter Cycling and Cycling Indices – may of course also be considered a network property. The chapter Indirect Effects in Ecology focuses on perhaps the most important network property: the presence of a strong indirect effect that in many cases may even exceed the direct effect.

The chapter Emergent Properties deals with the topic of emergent properties – the ecosystem as an integrated system is more than the sum of the components. The emergent properties are the result of all the system properties. Due to the synergistic effect of the network, autocatalysis, cycling, self-regulation and self-organization, and so on, an ecosystem acquires a number of very useful, holistic properties as a system – properties that are often called emergent properties. Self-organization itself is perhaps the most clear example of an emergent property. The chapter Self-organization looks into the emergent property of self-organization and how it is rooted in complex adaptive ecosystems. This chapter discusses how the spatial patterns, persistence, stability, and ability to develop and evolve can be explained as a result of the self-organization. The differences between ecosystems at an early stage and mature ecosystems can also be explained by self-organization.

Ecosystems are very complex systems. They have a large number of components with a large diversity, hierarchical organization, and nonlinear behavior. The chapter Ecological Complexity presents various aspects of ecological complexity, while the chapter Hierarchy Theory in Ecology presents the application of hierarchy theory in ecology. The hierarchical organization makes it possible to overview the complexity. It is also possible to get a better overview of the complex behavior of ecosystems by

Table 1 The five basic properties that are rooted in the 10 tentative fundamental laws encompass all the system properties presented

Basic property	*Derived system properties*
1. Ecosystems are open	The forcing functions (external variables) determine the ecosystem conditions
2. Ecosystems have directionality	Ecosystems show autocatalysis
	Ecosystems grow and develop
	Ecosystems have the propensity to maximize exergy storage and power
	Ecosystems have a body size pattern
3. Ecosystems have connectivity	The biotic and abiotic components of an ecosystem are connected in a network
	The network gives the ecosystem mutualism and synergy
	The indirect effect is significant due to the network and may even exceed the direct effect
	Ecosystems are self-organizing and self-regulated
	Ecosystems cycle energy, matter, and information
4. Ecosystems have emergent hierarchies	Ecosystems are organized hierarchically
5. Ecosystems have complex dynamics	Ecosystems grow and develop by increasing the biomass, the network, and the level of information
	Ecosystems are adaptive systems
	Ecosystems grow and develop and can cope with disturbances by a propensity to increase the exergy storage and the power
	Ecosystems, particularly under natural conditions, often have a large diversity, which gives the ecosystems a wide spectrum of different buffer capacities
	Ecosystems have high buffer capacities as a result of the complex dynamics
	Ecosystems recover usually rapidly and effectively after disturbances

use of goal functions and orientors that are presented in the chapter Goal Functions and Orientors. They are able to quantify the development of ecosystems as a result of the complex dynamics of ecosystems. One of the most useful orientors is exergy, which is presented in the chapter Exergy. The complex dynamics of ecosystems determine how they are able to develop and cope with disturbances. The exergy or energy that can do work of ecosystems – we cannot calculate exergy for an ecosystem due to its enormous complexity but we can calculate exergy for a model of the ecosystem – will have the tendency to be as high as possible under the prevailing conditions. Disturbances may of course cause a reduction in the ecosystem exergy, but the organisms try to organize themselves by their network and interactions to get the best out of the situation – it means in the Darwinian sense most survival, which may be expressed by exergy, as it covers the product of biomass and information of the ecosystem.

The five fundamental properties (see chapter Fundamental Laws in Ecology) cover *all* the ecosystem properties that are presented in the parts Ecosystems as Systems and Ecosystem Properties. An overview of the five basic properties and the derived additional system properties can be obtained from **Table 1**. Some of the properties are derived from more than one of the five fundamental properties, but to simplify the overview the derived system properties are associated with one of the basic properties. Particularly, the basic property that ecosystems have connectivity, which means that they form a network, and have a complex dynamics has been used to derive several system properties that could also be derived partly from one of the four other basic properties.

The chapter Overview of Ecosystem Types, Their Forcing Functions, and Most Important Properties, which is the last chapter in the part Ecosystem Properties, gives an overview of the 39 different types of ecosystems that are presented in the part Ecosystems. For all the 39 ecosystem types, the most important forcing functions are indicated, that is, the forcing functions (impacts) that may be considered a threat to the ecosystem or the forcing functions that most frequently determine the ecosystem function. It is possible to classify the forcing functions of the 39 ecosystems into four groups. The most basic properties of the four ecosystem classes are presented. They are the result of the prevailing conditions that are determined by the forcing functions. The most important properties are those that need to be maintained for the ecosystem to be able to meet the threats or those that are particularly important for the maintenance of the ecosystem function in spite of the impact.

The part Ecosystems has 40 chapters covering 39 different types of ecosystems. Most of the Earth's ecosystems are covered by the 39 types of ecosystems. A few rare types of ecosystems are not included, but all ecosystems frequently represented in nature are included. The ecosystems that are not included will however have properties close to one or more of the 39 types covered.

See also: Autocatalysis; Body Size Patterns; Cycling and Cycling Indices; Ecological Complexity; Ecological Network Analysis, Ascendancy; Ecological Network Analysis, Energy Analysis; Ecological Network Analysis, Environ Analysis; Ecosystem Ecology; Ecosystem Services; Ecological System Thinking; Ecosystems; Emergent Properties; Exergy; Fundamental Laws in

Ecology; Goal Functions and Orientors; Hierarchy Theory in Ecology; Indirect Effects in Ecology; Overview of Ecosystem Types, Their Forcing Functions, and Most Important Properties; Self-Organization.

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Ecosystem Ecology

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Introduction

Ecology is a broad and diverse field of study. One of the basic distinctions in ecology is between autecology and synecology, in which the former is considered 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, but 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**). This simple dimensional difference has served as an unfortunate divide between research conducted at the different ecological scales. While ecosystem ecologists maintain that it is always possible to convert species numbers into biomass or nutrient mass, population and community ecologists often feel that too much unique biological detail is discarded by abstracting to energetic or material units. The advantage of this abstraction, of course, is that energy and mass are conserved quantities, whereas number of individuals is not. Therefore, using conserved units it is possible to construct balance equations and input–output models. In fact, dimensionally, ecosystem ecology has more in common with organismal ecology in which the thermoregulation and physiology of a single organism is studied, which also often relies on energetic units. Indeed, all scales of ecological study have a role to contribute to general scientific understanding and have been developed to address a wide range of interesting and relevant questions regarding the natural world and the impact humans have on it.

History of the Ecosystem Concept

Systems concepts of the environment have long played a role in the development of ecology as a discipline, but these came to a head in the early twentieth century. During this period, the two dominant and competing ecological paradigms were the organismic (e.g., Clements) and individualistic (e.g., Gleason) views. The organismic approach held that communities and ecosystems were discernible objects that had an inherent and organized complexity resulting in a cybernetic and self-governing system, similar in ways to how an organism

Table 1 Typical dimensional units of study at different ecological scales

Ecological scale	*Dimensions*
Organismal ecology	d*E*/d*t*
Population ecology	d*N*/d*t*
Community ecology	d*N*/d*t*
Ecosystem ecology	d*E*/d*t*

d*E*/d*t* = change in energy over time; d*N*/d*t* = change in number over time.

regulates itself. The individualistic approach held that communities had observer-dependent boundaries and internal development was stochastic and individual. In this paradigm, the internal relations were synergistic, but not cybernetic since the individual parts functioned independently. The organismic ideas grew out of the functional understanding of whole systems such as lakes, and also out of the discussions involving how communities changed over time during succession. These ideas were influenced by philosophers of the day such as Jan Smuts. This was particularly true of German holists, such as the limnology group at the Kaiser-Wilhelm-Instituts in Plön led by Thienemann, and others such as Leick (plant ecology) and Friedrich (zoology). **Table 2** shows a summary of some of the main ecosystem and related concepts. This dialog between the holists and reductionists affected the main currents of ecological thought during this period, and it was in part resolved by the introduction of 'ecosystem', which is both physical in nature and also systemic.

The term ecosystem, which is ubiquitous today, both as scientific terminology and in common vernacular, grew out of this climate. It 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 and Cowles. While Tansley himself brought a systems perspective, the community as organism metaphor bothered him 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 thus, "… 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 70 years ago sounds fresh today, since it has changed little if at all. The major tenets of this approach are the explicit inclusion of abiotic 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 closely to the burgeoning disciplines of general system theory and systems analysis.

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 Forbes, Birge, and Juday in Wisconsin, and 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 and it has been applied to many habitats such as terrestrial, aquatic, and urban ecosystems.

Defining an Ecosystem

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

Table 2 Ecosystem and related concept

Year	*Term*	*Author*	*Concept*
1887	Microcosm	Forbes	Broadening of the biocoenosis concept
1914	Ecoid	Negri	Unholistic, based on Gleasonian ideas
1928	Ökologisches system	Woltereck	Still being used to avoid argument
1930	Holocoen	Friedrich	Holistic, biologistic
1935	Ecosystem	Tansley	Antiholistic, physicalist
1939	Biosystem	Thienemann	Stressing functional organization
1944	Geobiocönose	Sukacev	Geographic, landscape ecological
1944	Bioinert body	Vernadsky	Biogeochemical
1948	Biochore	Pallmann	Landscape ecological
1950	Landschaft	Troll	Holistic, 'Gestalt' viewing

Modified from Wiegleb G (2000) Lecture Notes on The History of Ecology and Nature Conservation.