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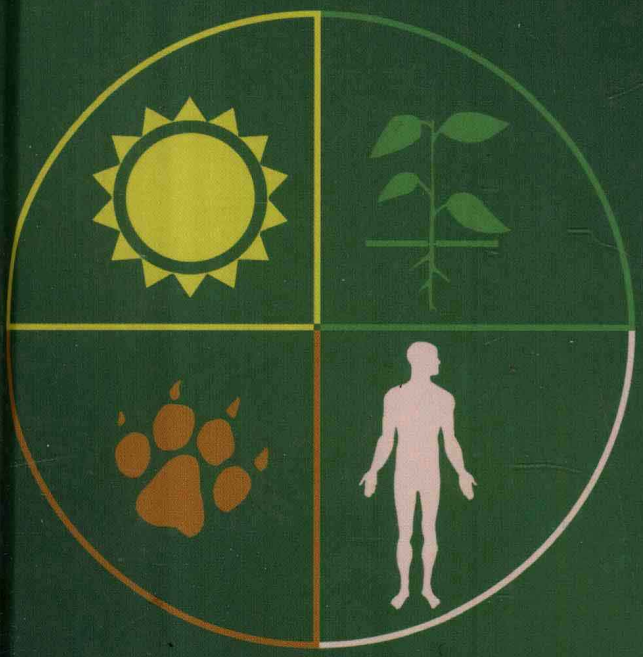
生态前沿系列

Ecosystem Ecology

生态系统生态学

Sven Erik Jørgensen



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评《生态系统生态学》

——衍生于《生态学百科全书》

牟 溥

（北京师范大学生命科学学院，北京，100875 E-mail：ppmou@bnu.edu.cn）

20世纪60～70年代，我国上上下下正在文化大革命中煎熬，百废待兴无望之时，世界生态学，尤其是生态系统生态学，却是如火如荼地发展。自从1935年英国生态学家Arthur Tansley提出生态系统的概念以后，随着将生物群落与其相互作用的环境结为一体而进行研究的逐步深入，生态系统和生态系统生态学的概念、定义不断完善；以生态系统为导向的生态学研究使得人们对生态系统结构、功能和动态的理解不断加深。值得提及的早期奠定生态系统生态学基础的研究包括：1942年Reymond Lideman发表的对温带淡水湖泊生物与生态系统能流的研究；1962年J. D. Ovington发表的将能量、水和养分运动结合起来对森林生态系统的研究；1959年Eugene Odum出版的*Fundamentals of Ecology*系统地阐述了生态系统生态学的理论，虽然许多观念现在看来有些片面；还有以F. H. Bormann和G. Likens为首的一批生态学家，在20世纪60年代早期开始的Hubbard Brook森林生态系统研究，他们首次利用小流域方法对森林生态系统进行全系统长期的定位和实验研究等等。对生态系统的深入理解促进了社会环境意识的高涨，生态系统生态学的完善使其成为生态学的主要分支之一，并成为方兴未艾的环境科学的理论支柱之一。生态系统生态学大发展的时期，我国的科学研究基本上处于停滞状态，因而国内的生态学家们缺乏对这门生态学分支的深刻理解与体会。我回国后与同事研讨时发现大家没有像国外同事那样大量自觉地运用生态系统概念来为科研工作导向，庶几与这些先天不足有关。

2008年，Elsevier出版集团出版了由丹麦生态学家Sven Erik Jørgensen主持编撰的3800页之巨的《生态学百科全书》，次年，该公司又出版了Jørgensen主编的《生态系统生态学》（衍生于《生态学百科全书》）一书。科学出版社决定将后者进行导读出版，当是为我国生态学者学习、探讨和理解生态系统生态学的极大帮助。虽然这本书只是将《生态学百科全书》中有关生态系统生态学的部分抽出编纂而成的一本书，但无疑这种处理使得关于生态系统生态学的信息集中、好用，毕竟在包罗万象的大部头工具书中查询不如专科工具书来得方便。

这本书的最大优点在于每个概念或词条自成一章，由对该领域有深入研究的专家撰写而成，内容充分、讨论深入，使读者对所感兴趣的概念或词条有较完整、深入的了解，并给出重要相关文献以备读者进一步探究。此外，编著者将收入的信息组合成三部分：1）作为系统的生态系统；2）生态系统特性；3）生态系统各论，从而将内容系统化，使全书不仅便于作为一本工具书，也像是一本教科书。

本书第一部分利用六章的篇幅介绍、评论生态系统生态学、生态系统思想、生态系统、生态系统服务以及生态学基本定律的概念、定义及其发展。第二部分用了十四章的

篇幅讲解生态系统特性，强调利用网络分析方法对生态系统功能进行分析研究。在这一部分，作者们对一些生态系统指数、综合特性、生态复杂性、阶层理论，尤其是生态系统能量性质作了较细致、深入的讲述。本书第三部分对编著者认定、选择的四十种具体生态系统类型进行了较细致的具体描述。这些生态系统基本上包括了全球自然、人工、水生、陆地及特殊生态系统类型。本人觉得，这一部分是本书最有使用价值、信息量最丰富的一部分。

编撰《生态学百科全书》是一项巨大的工程，要求其尽善尽美、面面俱到是苛求，但在浏览本书后，本人确有好则好矣，了却未了的感觉。也许是主编术业专攻的偏好，本书对生态系统能量分析、与能流功能有关的概念“非常重视”，而对过去几十年有广泛精到研究的生态系统物质（养分）循环及其相应理论、概念没有给予专门、系统的论述，遑论目前日益精准的能流、物质循环耦合研究发展起来的概念、理论。在本书前两部分的二十章中，没有一章专门讲述生物地球化学，这一直接源于生态系统生态学、并成为其最主要支撑的分支学科。在主编所撰第六章提出的他认为是形成生态系统理论的生态学十个基本定律中，基本上均可认为是能量导向的，仅有两个可以看到物质循环的影子。由于生态系统氮、磷循环是所有生态系统最重要的养分元素及其在系统中的复杂作用，在过去的几十年间受到生态学家们的关注最多，研究也最深入，结果也最为丰富，但在本书中，它们多在各论中散在论述，在前二十章里，鲜有提及。本书以生态系统能流为重，但书中出现“ecosystems cycle energy”（生态系统循环能量）（p. 3）这样的错误陈述，应予指出。也许作者确实有他的看法，但书中没有解释。

本书第三部分对选定的生态系统论述具体全面充分，图文并茂，信息量大，对读者了解某一、或某一类生态系统而言是一条捷径。尤其是各章论述中有大量生物地球化学信息，对前十八章中这方面的缺如也可以说是一种补救。但是整体上看，各具体生态系统的选择与综合平衡有待商榷的余地。在第三部分的四十章内容中，有八章论述人工生态系统，三十二章论述自然生态系统；十二章关于河流水体，六章关于湿地，六章关于森林，八章关于草原、荒漠、农业等矮植被陆地生态系统，八章关于其他系统。本人觉得既然将地中海类生态系统与地中海气候常绿硬叶林，荒漠与沙丘，沼泽与盐沼、淡水沼泽等均分章论述，是否也应该将温带针叶林、温带常绿阔叶林、温带针阔混交林分章论述？……当然，瑕不掩瑜，大多数章节论述还是相当不错的。本人的看法也只是代表个人观点。本人对本书前两部分的评论并未否认本书对生态系统能量学（ecosystem energetics）方面的许多精辟而深入的探讨。

本书可作为研究生生态课程的参考书，对于从事生态学教学和研究的教学和科研人员、生态学者有非常高的参考价值。

前　言

系统生态学，又称为生态系统理论，为生态系统如何作为系统运转提供了完整的理论。当然，当人们日渐频繁地用它来解释观察到的生态现象并用来协助进行环境管理，包括使用生态技术时，这个理论会不断被改善。生态系统理论发展到今天已经足够完整从而可以广泛地应用。仅从其应用的广泛性而言，或者说我们今天对一个理论的所有命题而言，生态系统理论有可能是有缺陷的，对其提出改进不应意外。

本书由三部分组成：第一部分作为系统的生态系统，着重于叙述生态系统的形态特性，包括在生态学的基本定律一章中陈述理论的基本科学命题。在第二部分生态系统特性中，对生态系统的整体性质给出更为综合、全面的表述。这些生态系统的整体性质，毋庸置疑，根植于系统特性之中，并且包括在这些命题之内。在第三部分生态系统各论中，分别概述了不同的生态系统。这些概述基于不同的生态系统特性，对各生态系统如何运转，以及科学命题如何应用于各生态系统加以阐释并说明它们的特性。

我希望本书能被生态学者和系统生态学者深入使用，从而对生态系统及其功能有较深入的理解，并为使生态学发展成为能够解释并预测生态系统响应的更为理论化的科学做出贡献。理论化发展的生态学将使生态学有可能以正确的理论思考取代许多通常耗费巨大的测量。

本书基于以下两点而成：

I. 系统生态学是一门生态学分支；

II. 最近出版的《生态学百科全书》通过大量插图对各种生态系统进行非常全面的概述。

由于《生态学百科全书》生态系统部分的编辑 Donald de Angelis 和系统生态学部分的编辑 Brian Fath 卓有成效的工作，才使得完整全面叙述所有生态系统以及最现代的生态系统理论成为可能。因此，我愿向 Donald 和全体生态系统词项的作者，Brian Fath 和全体系统生态学词项的作者表示感谢，感谢他们对《生态学百科全书》的贡献。本书对生态系统生态学这一非常重要的生态学分支进行了广泛和最新的叙述。《生态学百科全书》的出版极大地促成了本书的问世。

Sven Erik Jørgensen

哥本哈根，2009 年 5 月

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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

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（牟　溥　译）

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ECOSYSTEMS AS SYSTEMS

Introduction

S E Jørgensen, Copenhagen University, Copenhagen, Denmark

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.