ECOLOGICAL SYSTEMS

A Sourcebook of Concepts and Hypotheses

S. P. Madakan, A. U. Dzivama, J. O. Ihuma and U. N. Gadzama

Environmental Education Project (EEP) Publications

Abuja, Nigeria

Environmental Education Project (EEP)

ISBN: 978-35640-5-6

Cover Design: Abdulhakeem Bakare & S. P. Madakan
Printed by: BOAWOX

Cover picture: Hoopoe *Upapa epops*
Baobab *Adansonia digitata*

S. P. Madakan, A. U. Dzivama, J. O. Ihuma and U. N. Gadzama
Ecological Systems: A Sourcebook of Concepts and Hypotheses
First Edition
ISBN: 978-35640-5-6

ABOUT THE AUTHORS

Dr. Sunday Madakan is a Reader in Ecology in the Department of Biological Sciences at the University of Maiduguri, Nigeria, where he has been a member of faculty since 1986. He joined the University of Maiduguri as a Graduate Assistant in 1984. In 1985 he received a study fellowship award to study at the University of Aberdeen in Scotland where he graduated with a Master of Science in Ecology in 1986 and a Doctor of Philosophy in 1990.

Dr. Adamu Dzivama is a Reader in Bio-resources & Agricultural engineering at the University of Maiduguri. He is a Fellow of the Nigerian Institute of Engineers and has been teaching and practicing engineering for over 25 years. He obtained his Doctor of Philosophy from the University of Ibadan, Nigeria

Jerome Ihuma is a Lecturer in Ecology and Conservation Biology at the Department of Biological Sciences, Bingham University, Karu, Nigeria. He is currently working on his doctoral thesis which is nearing completion

Usman Gadzama is a Lecturer in Environmental Entomology and Molecular Biology at the Department of Biological Sciences, University of Maiduguri, Maiduguri, Nigeria. He is currently working on his doctoral thesis which is due to be completed by the end of 2015

The Earth from Space

Preface

Too often, prospective research students have approached us needing to do research but unable to identify any coherent issue that they would like to address. Most of these students do not have any idea of the key debates in their prospective fields of specialization and know nothing about the methods and technologies that could be used in research. It is in response to this that we have written this book. The book is intended to provide essential background for prospective research students (both undergraduate and graduate) interested in working in the fields of ecosystem and community ecology. The book is really an overview and therefore intended to serve as a starting point for further exploration of the subject.

Ecosystems comprise of two major components: the biotic (or living) and abiotic (non-living) components. The abiotic component of the ecosystem is essentially the conditions that exist in the ecosystem. These include the physical and chemical nature of the system and conditions such as temperature, water and nutrient availability within the system. These conditions influence and are in turn influenced by the way of life of the organisms (the biotic component) of that ecosystem. Traditionally, the study of ecosystems (ecosystem ecology) usually focusses on Nutrient Cycling and Energy Transfer. However, these two phenomena hinge on the biotic interactions that take place within the ecosystem and how these are influenced by the conditions within the system. The study of biotic relationships is known as community ecology and is usually treated distinctly from ecosystem ecology. Nevertheless, although this book is titled 'Ecosystems' we have included concepts in community ecology because we believe that these are essential for the understanding of ecosystems.

We start the book (Chapter 1) by reminding the reader that the study of ecosystems is a branch of Ecology and that the study of Ecology is crucial to the search for solutions to increasing environmental challenges faced by our planet today. The chapter concludes with a review of the concept of an ecosystem; including a brief history of how this thinking started in the field of Ecology. Chapter 2 introduces the fundamental concepts and principles necessary for postulating hypotheses and interpreting ecological phenomena. In Chapter three, we examine ecosystem state factors. These are the factors that combine to influence the state of an ecosystem through their effects on ecosystem control factors. In Chapter 4 we review the biotic mechanisms that drive ecosystems. Chapter 5 examines the primary ecosystem processes while Chapter 6 examines the major controls that determine how these processes proceed. The book ends with Chapter 7 which introduces the concept of ecological engineering and the rise of the engineering perspective in ecosystem ecology.

Acknowledgements

Many people have contributed in one way or the other in the making of this book. We are particularly grateful to the following people for suggestions that they made to improve the book: Yusuf Mohammed Yusuf, Saidu Baba, Peter Bzugu and Graham Davies. We are also grateful to the following all of whom we tremendously benefitted from having discussions with: S. S. Sanusi, W. S. Richards, S. D. Yusufu, Abba Umar, Mustafa Kokori, E. T. Rabo, Joy Turaki , Edith Anaso, R. T. Idowu, Sule Buba and Ahmed Abbator, all of the Department of Biological Sciences at University of Maiduguri. The first author will like thank the following for the enormous contributions that they made to his training as an ecologist while at the University of Aberdeen in Scotland. They are: George Dunnet, Charles Gimingham, Ian Patterson, Jean-Francois Giroux, Mike Swaine, Adrian Marshall, Mark Young, Martyn Gorman, David Raffaelli, John Ollason, Graham Pierce, Jose Limia, Chas Emes, Arnor Sigfusson, Colin Galbraith, Robert Donaldson, Peter Dewey, Augusto Vitale, Testfaye Amare, David Manyanza, Verena Keller, Humphrey Crick, Zubaid Akbar, Azarae Idris, Teresa Fernandes, Nick Brown, Mike Miltiadou, Gamil Attah, Carol Ritchie, Susan Marshall and Kathleen Lee. Many thanks to Professor Jean Bédard of Université Laval, Quebec, Canada who kindly gave me a grant to visit his laboratory and to Gilles Gauthier who provided a cordial and happy learning environment when I was in Quebec.

Table of Contents

Chapter 1: Introduction

1.1 THE STUDY OF ECOSYSTEMS: A BRANCH OF ECOLOGY

The study of ecosystems is a branch of Ecology known as Ecosystem (or System) Ecology. We will, therefore, begin the introduction to this book by reviewing the scope of the subject of Ecology in general. This is aimed at providing the background to the emergence of ecosystem ecology as a specific sub-discipline within Ecology. We then review the concept of an ecosystem; which is the basis upon which the sub-discipline of ecosystem ecology emerged.

Ecology has been defined in many different ways (see Box 1 for some definitions). Nevertheless, the following key inclusions, which are not disputed, are embedded or implied in all definitions. Firstly, it is generally agreed that ecology, as practiced today, is a science. A discipline is regarded as a science when its methods of inquiry and analyses are based on the scientific method (see Chapter 2 for a review of the scientific method). Secondly, there is no disagreement between ecologists that ecology is the study of the relationships that exists between living organisms and the environment in which they exist; and that these relationships determine the distribution and abundance of organisms in nature. The primary purpose of such a study, therefore, is to understand how the environment influences the capacity of organisms to survive and reproduce, and therefore to exist in the in specific habitats in the densities that they do and at the time that they do (the population ecology emphasis). Some would argue that such knowledge must be further synthesized to reveal how energy is transferred and nutrients are cycled for use by species (the ecosystem emphasis). In both cases progression into the study of the implications of the knowledge obtained is expected and for applied ecology it is the ultimate goal. Regardless of emphasis, the study of the interrelationships between organisms and their environment remains central in the definition of ecology.

The study of ecosystems is therefore a branch of ecology. In recent years, ecosystem ecology has become increasingly interdisciplinary incorporating approaches from a wide range of fields including economics, sociology, urban planning and engineering. We conclude this subsection by briefly looking at the discipline of ecology in general. In the next sub-section we briefly review the concept of the ecosystem in ecology

1.1.1. Origins of Ecology

The origin of ecology is in Natural History. Natural History is the predecessor of the present-day scientific discipline of Biology. Natural history, by definition, was not really a science. Natural historians recorded their observations of living things. These earlier observations later formed the bases for hypotheses testing approaches leading to the emergence of the scientific discipline of biology as we know it today. A consequence of this relationship is that the mother discipline of ecology is generally considered to be biology. In fact the underlying principles for understanding biological explanations of phenomena are exactly the same for biology as for ecology.

Right from the beginning of their existence; humans have always tried to understand the environment in which they lived. This was crucial for survival both in terms of obtaining food as well as protection from environmental dangers including those of predation, disease and hostile climatic conditions. It is therefore; fair to say that early humans needed to develop ecological knowledge in other to survive. Some have argued that the discipline of ecology is therefore as old as humans themselves.

BOX 1: DEFINITIONS OF ECOLOGY

1. Ernst Haeckel (1869): The total relations of the animal to its organic and inorganic environment. Although this definition focused on animal ecology, it actually reflected system ecology because of its reference to the connectedness of the organic and the inorganic environment.
2. Charles Elton (1927): He defined ecology as "scientific natural history". By using the term "scientific", Elton's definition set a minimum standard on how ecology is to be conducted. Prior to this definition many studies that qualified as ecology were simply descriptive. This definition required that ecological studies be conducted in a systematic way with the intention of testing hypotheses.
3. Andrewartha (1961): The scientific study of the distribution and abundance of organisms. This definition leans towards population and community ecology perspectives. It, however, recognizes that the ultimate outcome of all ecological processes is on the number of species, the number of individuals within species and where they can establish themselves successfully.
4. Krebs(1972, 2008): "the scientific study of the interactions that determine the distribution and abundance of organisms".
5. Townsend *et al*. (2003) "the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance."

Like our ancestors, modern-day humans continue to face the challenges of having to obtain enough food to feed its populations across the globe. But our problems have since been compounded. Our problem is no longer just how to feed ourselves. Humans now have to battle with how to deal with major changes that our actions are causing to the global ecological processes. Our need for a better understanding of the functioning of global ecological processes has never been more pressing

1.1.2. Branches of Ecology

Ecology has been approached in many different ways and new branches continue to emerge as new perspectives to the understanding of ecological phenomena are identified. Mainstream branches of ecology are based on traditional biological organization that identifies strata of biological study from the molecule to the system. Using this perspective, biology is classified into molecular, organismal and system levels of study. These categories coincide with the levels of biological organization namely: molecules, cells, tissues, organs, organ systems, organisms, populations, communities and ecosystems. Many branches of ecology are based on this perspective. Examples of branches based on biological hierarchy include Behavioral ecology and Physiological ecology (organismal level), Population ecology (population level), Community ecology (system level) and Ecosystem ecology (system level).

Branches of ecology based on biological organization arose in response to the fact that each level of biological organization possesses certain emergent characteristics and properties that could not be studied at other levels. For example, a population by definition is made up of just one species; as a result of this the trophic relationships that exist in a community cannot be studied at population level. Such relationships can only be studied at community level. Thus, trophic structure is an emergent characteristic that can only be observed if the ecologist treats a group of several species as the unit of study (community ecology).

.

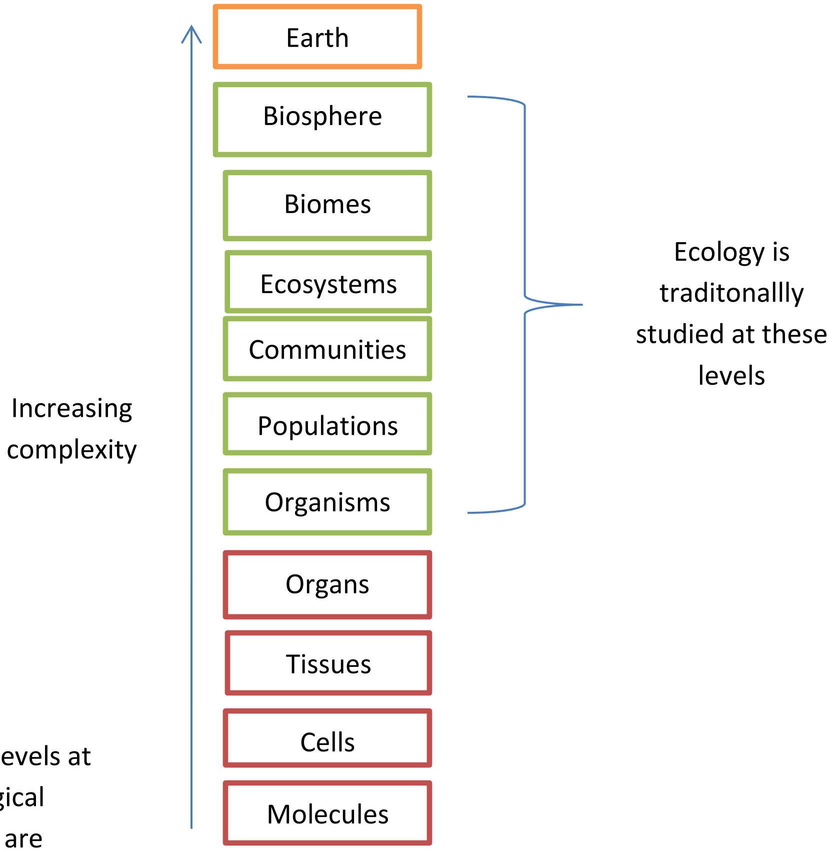


Figure 1.1: Levels at which biological phenomena are studied

Not all branches of ecology are based on biological organization; some branches are based on taxonomic groups (e.g. Bird ecology, Microbial ecology, Mangrove ecology etc.) Some are based on habitat type or environment (e.g. freshwater ecology, soil ecology, forest ecology etc.). Other branches of ecology include those based on processes (e.g. decomposition ecology, fermentation ecology, industrial ecology)

1.2 THE CONCEPT OF AN ECOSYSTEM

The term ‘Ecosystem’ was first used, in a publication, by the British ecologist A.G. Tansley in 1935. The term is believed to have actually been coined in the early 1930s by A.R. Clapham a young man at the Department of Botany at Oxford University in England (Willis, 1997). The German entomologist Karl Friedrich had introduced the word *holocoen* for the concept in 1927. Later, in 1944, the Russian forest ecologist Vladimir Sukachev introduced term *biogeocoenosis*. However, “ecosystem” is now the universally accepted term.

At the time of Tansley’s publication, ecology, and biology in general, was dominated by the organismal perspective. In his ground-breaking paper, which addressed the use of concepts and terms in vegetation studies, Tansley wrote:

“Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment with which they form one physical system”.

Tansley saw organisms integrated with their physical environment into a system “in the sense of physics”. He called these systems “ecosystems” and regarded them as “the basic units of nature”.

The underlying assumption in the concept is that natural environments have the tendency to repair themselves after sustaining damage. In other words, after being subjected to change, natural environments tended to revert to the original state in which they were if given enough time to recover. This view of the dynamics of natural systems was already widespread prior to the use of the term “ecosystem”. Tansley, therefore, simply gave a name to a concept that was already being debated. For example, Frederick E. Clements (1905, 1916) and Charles Elton (1930) had already been talking about successional change in plant and animal communities respectively. Box 2 gives a summary of some of the key milestones in the history of the development of the concept of an ecosystem.

The ecosystem view was in recognition of the need to view nature in a holistic way i.e. that it was necessary not only to study the components of nature but to understand how these components are linked. This was the only way in which the consequences of events affecting the natural environment could be determined.

The ecosystem concept was tremendously boosted by the rise of systems analysis which occurred in the late 1940s after the Second World War. Systems analysis, with its machine analogy, was particular amenable to the analysis of natural systems; which are inherently complex.

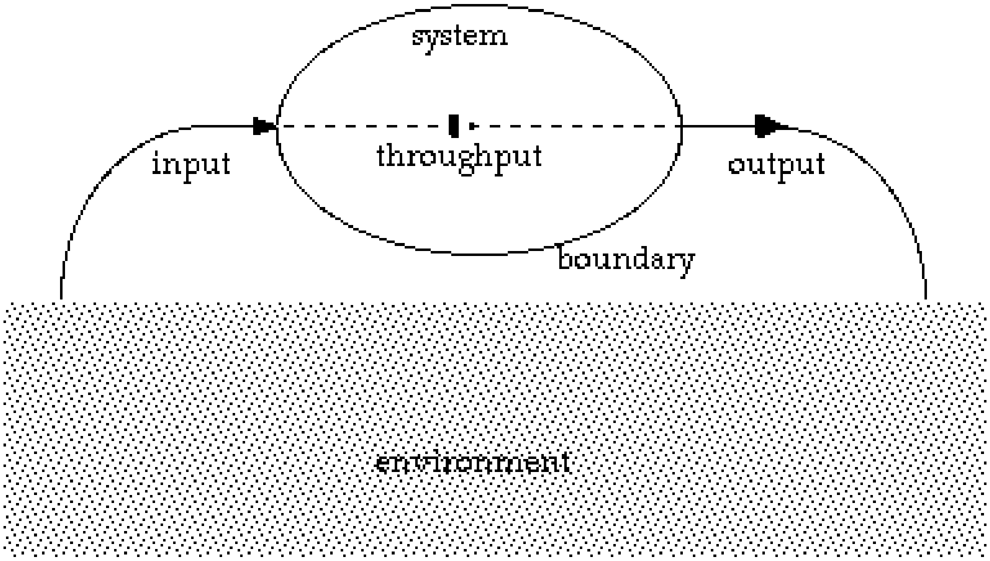


Figure 1.2a: The Basic Concept of a System

Box 2: Milestones in the development of the ecosystem concept

1858 – Alfred Russel Wallace sends his manuscript presenting his conclusions concerning species origin and diversity to Charles Darwin. Darwin had been working on a similar idea but was yet to publish it.

1859 – Charles Darwin publishes the ‘ On the Origin of Species …” which outlined the interrelationships of living organisms with themselves and the abiotic environment in which they live. Darwin focused on how organisms struggle for survival in their environment through adaptation driven by natural selection.

1865 – German physicist Rudolf Clausius introduces the concept of entropy. This concept is later formalized as the second law of thermodynamics and will come to greatly influence the thinking of early ecosystems ecologists like Chancey Juday and Raymond Lindeman

1895 – Danish plant ecologist Johannes Eugenius Warming publishes *Plantesamfund: Grundtraek af den okologiske Plantegeografi* “Oecology of plants: an introduction to the study of plant communities. Warming’s work was pioneering in the understanding of plant communities and how these are determined by environmental factors.

1899 – Henry Chandler Cowles - His work shade more light on the dynamic nature of vegetation arising from a combination of biotic and abiotic interactions.

1913 – Josias Braun-Blanquet – Recognized the roles of both competition and edaphic factors in determining floristic composition

1916 – Frederic Edward Clements. – Clements introduced the concept of climax community.

1926 – American botanist Henry Gleason presents an alternative view to F.E. Clements view of plant communities

1926 – German limnologist August Thienemann publishes a food web of lakes and develops the concept of nutrient cycling

1926 – Russian Vladimir Verdansky develops the modern concept of the biosphere

1927 – Charles Elton introduces the concept of a food chain.

1935 – The term “Ecosystem is first used in literature by British Ecologist Arthur Tansley

1940 – American aquatic ecologist Chancey Juday publishes a study of the energy budgets of lakes. Juday developed the concept of primary production

1942 – Raymond Lindeman – introduced the trophic-dynamic model and emphasized bottom-up energy flow

1953 – Eugene Odum – describes community stability in terms of energy

1957 – Howard Odum – Measures primary production

The machine analogy inherent in systems analysis enabled ecologists to start to view ecosystems in terms of the outcomes that they produce. From the holistic view that is the ecosystem concept, the combined effects of the biotic and the abiotic environments culminate into two primary outcomes: energy is transferred between pools and nutrients are cycled. It is these two processes that determine capacity of ecosystems to support life and how nature is structured.

Once this perspective became established, it quickly became obvious that an appropriate currency for assessing ecosystem functioning is energy. The first ecologist to introduce the use of energy as the currency for ecosystem assessment was Raymond Lindeman. In his paper on the trophic-dynamic aspect of ecology Lindeman (1942) drew attention to significance of energy transfer from one part of an ecosystem to another and categorized organisms within ecosystems according trophic levels of producers, consumers and decomposers through which energy is transferred. Today the transfer of energy, along with nutrient cycling, still remains central to the understanding of ecosystem function and structure.

Over the past decades it has become obvious that the ecosystem approach offers the best way to understand how nature provides the essential services that support life on earth. The ecosystem approach is fundamental to the management of our planet's resources it is the integrated links between organisms and the physical environment that are responsible or producing conditions that support life on Earth. It is also these processes that are responsible for resources that humans use as food, fuel, fiber and medicines

1.3 PRACTICAL VALUE OF THE ECOSYSTEM APPROACH

Virtually all the international conventions aimed at sustainable utilization of natural resources are now based on the sustenance the Earth's essential ecosystem services. One of the main reasons for this shift in perspective is that early models, mostly based on population dynamics, such as the maximum sustainable yield (MSY) model in fisheries failed woefully to prevent overexploitation. The MSY approach was species-based and did not adequately account for the complex interactions that come into play in determining ecosystem outcomes.

Ecological systems are responsible for the provision of ecosystem services. The term ecosystem services refers to a wide range of processes through which natural ecosystems help sustain and fulfil human life. These services include the maintenance of biodiversity and the production of goods, such as food, fuel, fiber, pharmaceuticals and other industrial products. In addition to the provision of goods ecosystems support life through the provision services including, water and air purification, flood and drought mitigation, soil formation and preservation, soil nutrient content maintenance, waste decomposition and detoxification, pollination and dispersal and many others.

1.4 A FRAMEWORK FOR STUDYING ECOSYSTEMS

Ecosystems are complex systems. One of the reasons why it has been so difficult to understand ecosystem functioning is the wide array of interacting variables that come into play under any given circumstance within ecosystems. A useful framework for studying the structure and functioning of ecosystems is based on Amundson and Jenny (1997). They identified at least five independent control variables, which they called state factors that control the structure and functioning of ecosystems. These are climate, parent material, topography, potential biota and time. These state factors (outer circle of Figure 1.2b) control ecosystem processes through their influences on five interactive controls (inner circle of Figure 1.2).

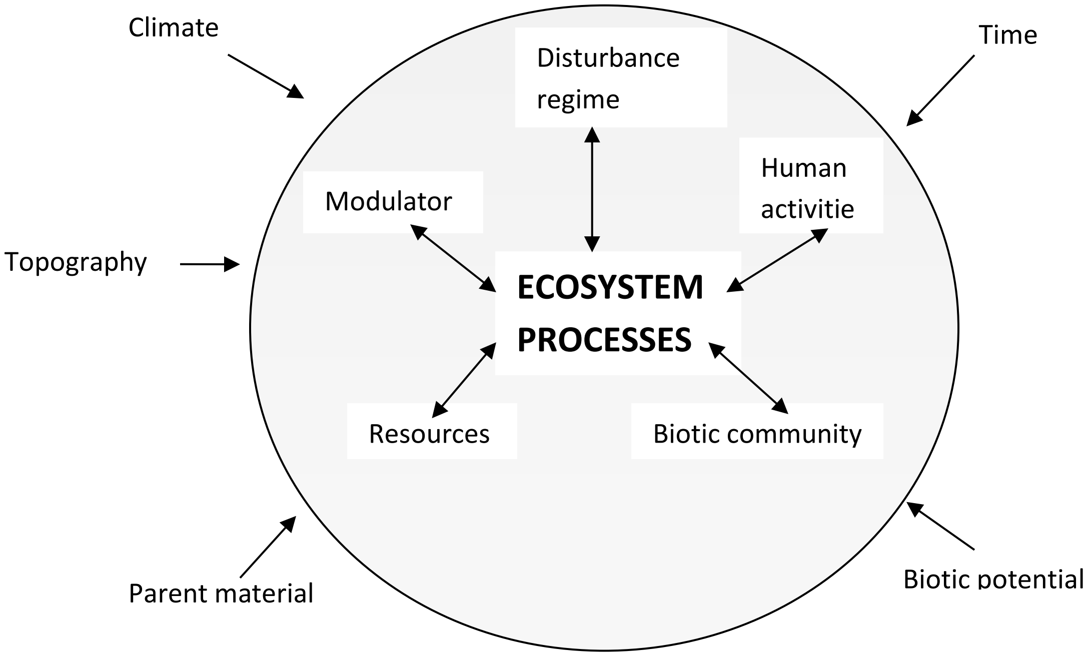


Figure 1.2b: Ecosystem state factors (outer circle) and their relationship with interactive controls (inner circle) on ecosystem processes. (Adapted from Chapin *et al*, 2002; based on Jenny (1941) and Amundson and Jenny (1997)

At the global level, climate appears to be the most influential state factor. Its effect determines the distribution of the Earth's major biomes. At local levels, topography and parent material combine to influence distribution and abundance through their effects on microclimatic conditions. It is these conditions that combine with time (evolutionary time) to determine which species from the potential biota form the biotic community of the ecosystem. In the rest of this book we examine ecosystem structure and function using this basic framework.

Chapter 2: Underlying Concepts

2.1 EVOLUTION AND NATURAL SELECTION

Biologists attribute the wide range of diversity of life that exists today to a process called Evolution. The theory of evolution was first put forward by Charles Darwin and Alfred Wallace about 150 years ago. In 1859, Darwin published his famous book *On the Origin of Species by Means of Natural Selection* in which he articulated what later became known as Darwin's theory of evolution through natural selection. One of the most quoted statements in biology is "nothing in biology makes sense except in the light of evolution". This statement is attributed to the geneticist and evolutionary biologist Theodosius Dobzhansky. Dobzhansky's argument is that patterns in nature can only be explained based on the assumption that they have come about as a result of evolution through natural selection. Ernst Haeckal must have had the same thought in mind when he coined the term 'ecology'. Haeckal's definition of ecology was explicitly evolutionary. He wrote: "By ecology we mean the body of knowledge concerning the economy of nature – the investigation of the total relations of the animal both to its relations with other animals and plants with which it comes directly or indirectly into contact – in a word, ecology is the study of all those complex interrelationships referred to by Darwin as the conditions of the struggle for existence". Most ecological hypotheses are based on the underlying assumptions of evolution and natural selection. It is therefore imperative for students of ecology to have a complete understanding of this concept.

2.1.1. Evolution

Darwin's theory of evolution contained five different aspects. Some authorities consider each of these aspects as separate theories on themselves. These are: Perpetual change, Common descent, Multiplication of species, Gradualism and Natural Selection.

Perpetual change

This is the basic aspect of evolutionary theory on which the others are based. It states that the living world is constantly changing. In other words, the properties of organisms are constantly undergoing transformation over generations as time passes.

Common descent

Another aspect of the theory of evolution is that of common descent. According to this proposition all forms of life on earth descended from a common ancestral form. A great deal of work has been conducted to investigate this proposition since Darwin made it. During this time some biologists have proposed an alternative proposition suggesting that different forms of life arose independently and descended to the present linear unbranched genealogies. Comparative studies of organismal form, cell structure and molecular biology so far seem to support the common descent proposition.

Multiplication of species

According to Darwin's theory, new species arise when old ones are split or transformed. Species are reproductively distinct populations of a type or range of organismal forms. Darwin's "multiplication of species" is now referred to in modern literature as speciation. Speciation occurs when populations evolve reproductive isolation mechanisms. Such isolation can be prezygotic or postzygotic. Prezygotic isolation is when barriers act to prevent fertilization. Postzygotic isolation occurs when hybrids are inviable or sterile. Several modes of speciation have been described. These include allopatric speciation, peripatric speciation, parapatric speciation and sympatric speciation. Allopatric speciation occurs when isolation or divergence takes place. Isolation is created when gene flow is reduced or eliminated. Divergence is the result of mutation, genetic drift and selection acting on populations separately. Peripatric speciation is a special version of allopatric speciation and happens when one of the isolated populations has very few individuals. In parapatric speciation reproductive isolation occurs without complete isolation. Thus some gene flow is maintained. In sympatric speciation reproductive isolation evolves with complete geographic overlap. The evolutionary processes involved in speciation are mutation, natural selection, sexual selection and random genetic drift.

Gradualism

According to this aspect the large anatomical differences that we see between different species arise as a result of gradual accumulation of small incremental changes over very long periods of time. Gradualism is an important concept because genetic changes that have very large effects on organismal form tend to harmful to the organism. Gradualism does not, however, rule out the possibility of occasional occurrence of large effects that are sufficiently beneficial to be favored by natural selection.

2.1.2. Natural selection

Darwin referred to the primary mechanism of evolution as Natural Selection. Natural selection theory can be broken down into three distinct propositions as follows:

(i) Individual organisms within a population (species) differ from one another in morphology, physiology and behavior and much of this variation is inherited

(ii) Populations have the potential to grow exponentially but are not able to do so because of environmental limitations e.g. competition for resources, predation and disease, harsh environmental conditions.

(iii) Some inherited characteristics increase the probability of survival and reproduction of the individuals that bear them. Consequently, their descendants (which also bear these traits) come to make up an increasing proportion of the population with every new generational change

The outcome of the natural selection process is that organisms tend to be found in environments in which they have adaptations to survive and reproduce. In other words the distribution and abundance of species in nature is determined by the adaptations that they possess and these adaptations are a consequence of natural selection.

To increase our understanding of natural selection, let us consider some examples of adaptations. If one looks at an organism and consider its traits (i.e. color, size, shape, behavior, biochemistry) and how the traits function, it is obvious that many of them appear to favor the survival and reproductive capacity of the organism in the environment in which it is naturally found. As a result of this fit that the organism has with its environment, we say that the organism is adapted to its environment. However, to understand these traits as adaptations, it is necessary to understand what is meant by the environment of an organism. The environment of an organism may be defined as anything in the surrounding of the organism that can affect its survival, growth and reproduction. The environment comprises of living (biotic) and non-living (abiotic) components. The biotic environment of an organism includes all other organisms that affect its survival, growth and reproduction. These include competitors, predators, parasites, disease and symbionts. The abiotic component includes conditions in the environment such as temperature, humidity, salinity and its physical characteristics. The following examples of adaptation may help shade more light on the mechanism of natural selection.

- Adaptation of plant leaf size to climatic conditions
  Plant leaf size and structure shows adaptation to climate. An example of this can be seen in desert plants. Desert plants exhibit a wide range of leaf adaptations to the dry and hot environment prevalent in deserts. Some plants have small leaves which are hard and coated against water loss. Still in the desert other plants have succulent stems in which water is stored. Other plants, also in the desert, such as cacti have reduced leaves and succulent stems and in so doing drastically reduce water loss from leaves while storing water in their stems. In contrast to the desert flora, plants in the tropical rainforest tend to have very large leaves with pointed tips to promote runoff from leaves; an adaptation that is essential to prevent waterlogging on leaves (a situation that not only reduces physiological efficiency but also promotes the proliferation of disease).

- Adaptations relating to herbivory
  Many plant species have developed adaptations against herbivores that feed on them. These include morphological features such as thorns and biochemical features such as toxins. The evolution of these features has created an environment in which herbivores have been

selected to be able to eat plants despite these deterrents. Many herbivorous insects, for example, have evolved biochemical mechanisms for detoxifying specific plant toxins. Note that in this example first a trait evolved in plants because of the insects then a trait evolved in the insects because of the new trait in the plants; since this involves species evolving traits in response to one another it is an example of a process known as coevolution. Coevolution may continue in this way with plants evolving alternative toxins that could not be detoxified by the insects and so on.

- Adaptations for mutualism
  Species interact with each other in other ways than feeding. Flowering plants and pollinating insects, for example, are coupled in mutualistic relationships. The pollinating insects transfer pollen from flower to flower, thereby facilitating sexual reproduction. Mutualists such as these may evolve traits in response to one another. Many flowers, for example, have evolved combinations of color, shape, size and odor that attract specific kinds of pollinators. Such flowers are said to be adapted to attract a specific pollinator.

2.2 THE SCIENTIFIC METHOD

Ecology is a science. This means that all ecological investigations are conducted in a scientific manner. There are many variants of the scientific investigation process. The basic framework (Figure 2.1) is, however, the same in all cases.

Usually an observation is made or a situation is imagined (inspiration). In many cases inspiration is a result of observation and inquisitiveness. After the observational/inspirational phase, the steps that follow may vary a bit depending on the nature of the problem or the manner in which it is being investigated. The steps taken by theoretical /mathematical ecologist are usually slightly different from those of empirical ecologists and applied ecologists. Theoretical ecologists use mathematical and computer simulation tools to predict ecological phenomena. Empirical ecologists conduct experiments leading to the identification of regularities and relations in nature. These patterns are then used by theoretical ecologists to refine their assumptions and to develop new and more models. Empirical ecologists also test the predictions of theoretical models. Another group of ecologists are the applied ecologists. Applied ecologists focus on the development of solutions. They use ecological knowledge to develop new products and procedures.

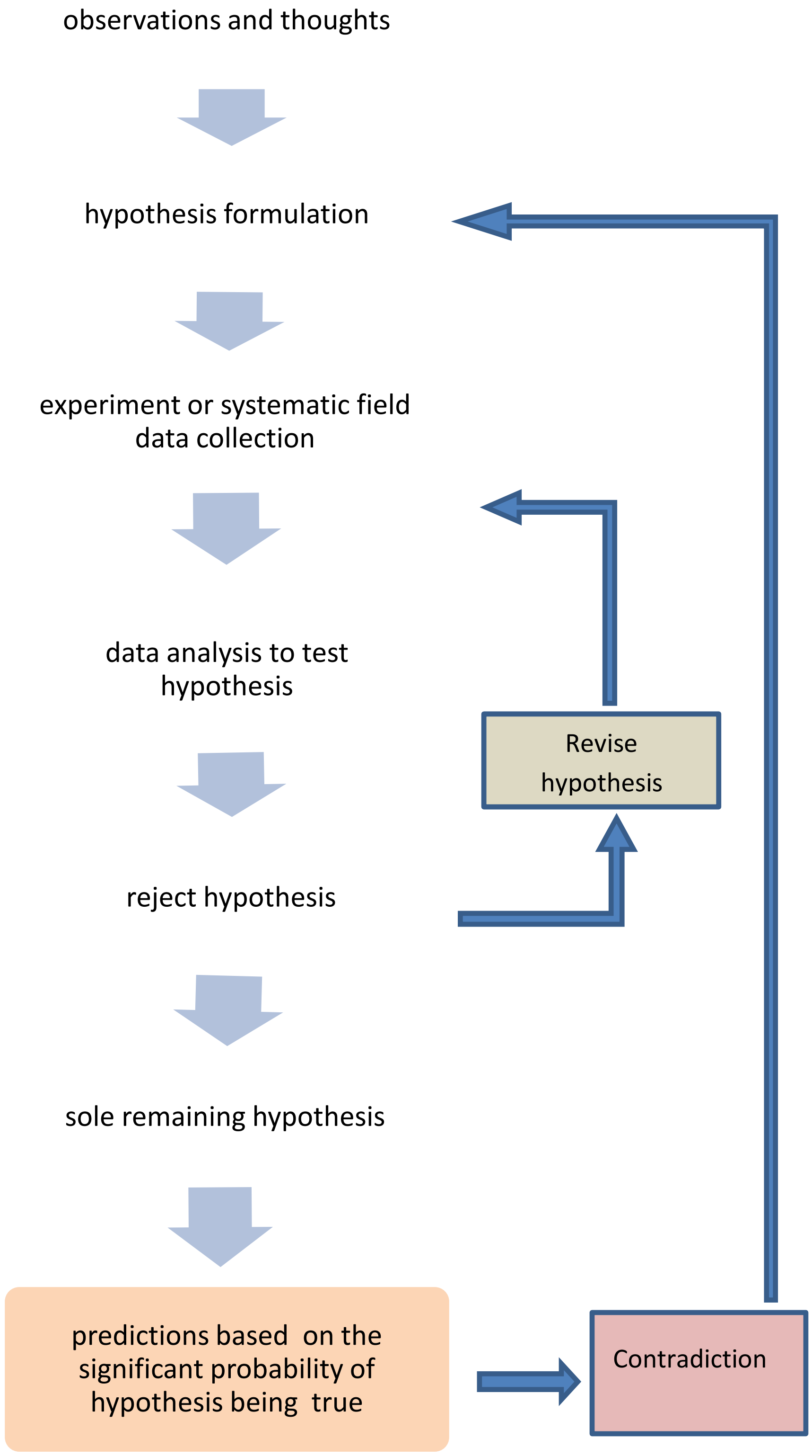


Figure 2.1: Basic framework for the scientific investigation process

In each of the above cases, scientific investigation (although retaining its basic framework) may proceed through very different stages. Below are examples of the stages that each may follow:

- Empirical investigation:
  - Stage 1: Observe a phenomenon
  - Stage 2: State a hypothesis. The hypothesis must be falsifiable.
  - Stage 3: Design an experimental procedure or measurement regime that allows the collection of measurements that can used to for statistical testing of the hypothesis
  - Stage 4: Statistically analyze the data to test the hypothesis
  - Stage 5: Refine and correct the hypothesis and continue if necessary
- Theoretical investigation
  - Stage 1: Identify a regularity or relation discovered through experimentation
  - Stage 2: Build mental pictures and develop a hypothesis about the origin or nature of regularity or relation
  - Stage 3: Identify basic mathematical relations from which regularity may result
  - Stage 4: Use analytical or numerical tools to determine whether experimental regularities result from the starting mathematical equations
  - Stage 5: If incorrect, find new mathematical starting point
  - Stage 6: if correct, predict new regularities to expect in future empirical investigations
- Applied ecology : development of a product or process
  - Stage 1: identify a product or process that is required
  - Stage 2: Design a set of procedures
  - Stage 3: Build apparatus
  - Stage 4: Determine whether proposed methods produce the desired outcomes
  - Stage 5: If not, modify and continue modification until desired outcomes are obtained
  - Stage 6: if methods produce results then optimize procedure with respect to speed, cost, environmental impacts and other factors
  - Stage 7: Make product or process available (as a free service to humanity or for commercial gain)

In situations where experimentation is required, the effects being tested are usually induced by the researcher. There are situations, however, where the researcher is interested in investigating effects which have occurred naturally. In such situations, the research collects data in such a way that it becomes possible to test hypothesis using measurements from areas where the effect has taken place and comparing these with measurements from similar areas where the effect has not occurred. Ecologists call these situations natural experiments. For example, an ecologist may collect information on the effect of a natural or accidental fire in a forest reserve by taking measurements in patches that were affected by fire and comparing these with measurements from patches that were not affected by fire. In such a situation the effect of the fire has resulted in a natural experiment. In a natural experiment the ecologist did not deliberately induce the effect, it occurred naturally. Another example is the opportunity provided for studying primary succession when volcanoes erupt. Volcanic eruptions give opportunity to ecologists to study primary succession because lava from the volcanic eruption did not contain any seed bank. As a result, the first vegetation to arise on areas covered by lava started a process of primary succession. Usually, however, scientific hypotheses including those of ecology are tested through experiments in the field or laboratory in which the treatments (the effects being investigated) and the controls are designed and laid out by the scientists themselves.

At this stage you may be wandering what to make of all those student projects presenting a great deal of information obtained from observations in which no hypothesis was tested. The answer to your question is that these categories of studies cannot be regarded as complete scientific studies on their own. However, they can be of value when it comes to formulating hypotheses because they provide the background observations that are necessary for this. In other words they belong to the first stage in the stages of scientific investigation. Most institutions of higher learning will only award Bachelor and Master of Science degrees to their students if the dissertations presented qualify as proper and complete scientific investigations.

Topograhy is an important ecosystem state factor (Picture: S. P. Madakan)

Chapter 3: Ecosystem State Factors

3.1 OVERVIEW

Ecosystems consist of components which are living as well as non-living. The living components constitute the biotic environment while those that are non-living constitute the abiotic environment within an ecosystem. Ecosystem ecology differs from other branches of ecology because its focus is on the interactions between the living and the non-living components as an integrated system. The central theme in ecosystem ecology is to understand the factors that regulate quantities and flows of energy and materials within and between the biotic and abiotic components. These quantities exist in biotic and abiotic pools or reservoirs that are linked through the fluxes or flows energy and materials. Materials crucial to ecosystem function include water, carbon and nitrogen as well as rock-derived elements (e.g. Phosphorus) that are essential to the metabolism of living things. Also present in these pools are a wide range of chemicals that have been artificially introduced into the system as a result of human activities. These chemicals include pesticides, radionuclides and a wide range of others, some of which are xenobiotic. The major abiotic pools include soil, sediment, rocks, water and the atmosphere. The biotic pools are the living organisms that inhabit these abiotic pools. They include all organisms belonging to the three domains of living things, namely: Archaea, Bacteria and Eukarya. Materials and energy flows within an ecosystem take place as a result of key processes. These processes include photosynthesis, consumption, decomposition and absorption. Photosynthesis drives primary production in which solar energy and carbon from carbon dioxide and nutrients absorbed from water or soil are used in primary production of biomass. Other organisms they consume this biomass through either herbivory, carnivory or detritivory. Death organic matter is decomposed into inorganic matter by other organisms (bacteria and fungi) during their own nutritional processes leading to the release of inorganic chemicals into the soil or water to be reabsorbed into the system by primary producers. In addition to decomposition, rock-derived chemicals are also released into the system through physical processes such as weathering. Interactions that take place in ecosystems link the biotic component to the physical systems on which they depend.

Interactions between the biotic and abiotic components combine to create conditions that exist within the ecosystem. These conditions constitute part of the abiotic environment of the ecosystem at the local level. At regional and global levels, ecosystem conditions are dictated primarily by climate. Abiotic conditions exert their influence on ecosystem function through their effects on the physiology at the organismal level. These physiological effects in turn influence population processes that govern the population densities and age structures. At the community level, they act on biotic interactions that determine which species are present and the rates at which they consume resources. In this chapter we review the key abiotic factors that modulate biotic function in ecosystems.

According to Chapin *et al* (2002), ecosystem structure and functioning are governed by at least five independent control variables. These five variables, referred to as state factors (Amundson and Jenny, 1997) are climate, parent material (via soil), topography, potential biota (organisms with potential to occupy a site) and time (Figure 1.1). It is these factors that work together to determine the characteristics of an ecosystem. Climate, parent material and topography are abiotic and physical in nature while potential biota constitutes the biotic component of the system. Time is relevant in the context of temporal changes that take place within the system. Parent material is determined to a large extent by the geology of the region. In effect abiotic factors affecting ecosystem can be reviewed under three major categories namely: climate, geology and soils and topography

The concept of ecosystem state factors is based on the state factor model of systems analysis which has its origin from the discipline of pedology. A key requirement of system state factors is that they are independent of the system which they influence. Amundson and Jenny (1997) argue that this requirement is unimportant for ecological studies dealing with landscape segments such as sites or plots. They also argue that state factors may, in many locations and for certain periods of geological time, vary independently of one another. According to them, this independence allows the possibility of teasing out and quantifying the influence of one state factor at a time on ecosystem properties. They defined the relationship between state factors (independent variables) on the properties (dependent variables) of an ecosystem in mathematical form as:

Ecosystem properties = f (climate, topography, organisms, parent material, time, humans, …)

Several approaches have been proposed for teasing out the influences of state factors on ecosystem properties. These include the use of chronosequences and toposequences. Chronosequences and toposequences allow researchers to compare sites that are as similar as possible in all respects except for one factor. A chronosequence is a series of sites of different ages which are located in similar climatic conditions and have similar topography, parent material and the potential to be occupied by the same species of organisms. In a toposequence analysis sites that are similar in respect all respects except topography are compared.

In the next few sub-sections we briefly examine each of the major state factors identified by Amundson and Jenny (1997).

3.2 CLIMATE

Climate is defined as the annual pattern of temperature and precipitation at a given location. Patterns of climate are vital to understanding global patterns in the distribution and abundance of species on Earth. Climate is determined largely by three general components of the physical environment on Earth. These are energy, water and atmospheric gases. These three components interact with the Earth's shape, gravitational pull, rotation, revolution and angle of tilt to form the various physical environments and climatic variations observable on the planet. The consequence of this interaction is that the Earth exhibits complex patterns of circulation because of two major reasons. Firstly, differences in solar radiation inputs into the Earth's environment occur due to the effects of latitude (shape of the Earth) and season (tilt of the Earth). Secondly, the Earth's rotation produces daily variations in temperature and forces on atmospheric gases. It also produces annual variation (seasons). This is illustrated in Figures 3.1 and 3.2.

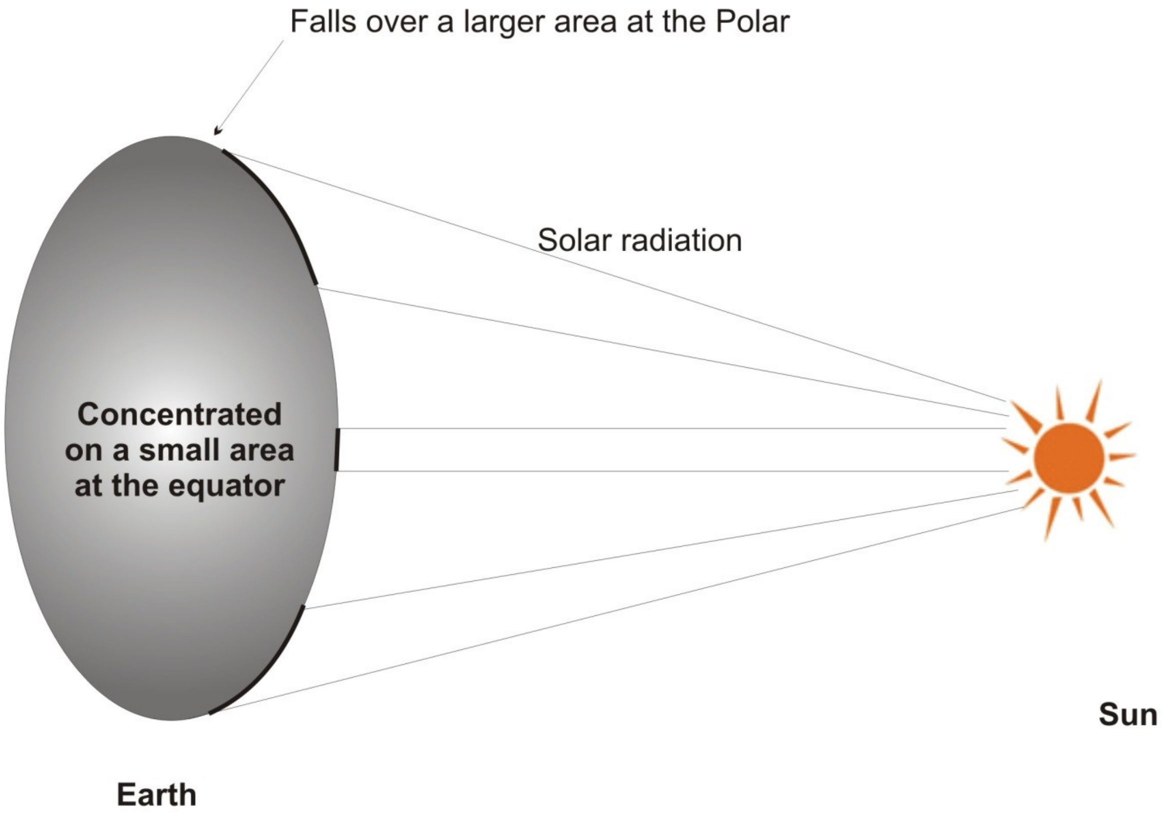


Figure 3.1 Solar radiation is highest at the equator than at the polar regions

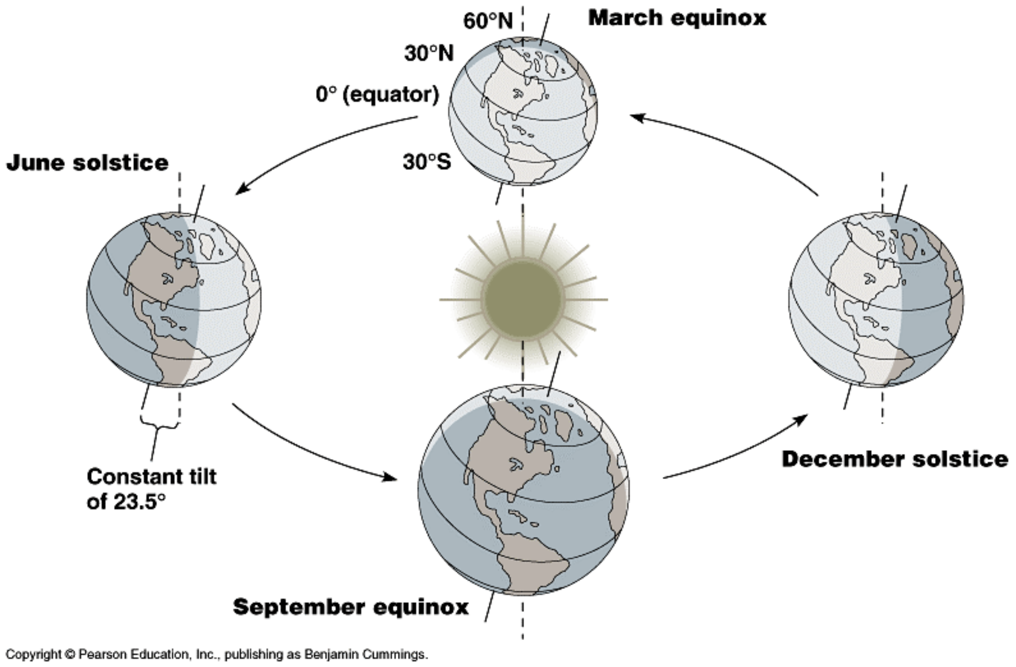


Figure 3.2 Tilt and rotation of the earth creates seasons (Copyright: Pearson Education Inc.)

The above phenomena combine to produce climatic regions on the globe each with its peculiar conditions to which occupying organisms have to withstand. In the rest of this chapter, we will briefly review how interactions between the Earths physical characteristics combine to determine the patterns of energy, water and atmospheric gases and therefore the climatic regions on the planet.

Solar radiation is the major determinant of the climate of the Earth. As a result of the Earth's spherical shape, its tilt on its axis and the fact that it revolves around the sun, more solar radiation strikes the Earth at some latitudes and at more times of the year than in others. Furthermore, the seasonal variation in available solar radiation depends on latitude. It is these imbalances in the amount of solar radiation reaching different parts of the planet that drive the movement of water (ocean currents) and atmospheric gases (winds) with profound effects on precipitation and temperature in the various climatic regions.

3.3 PARENT MATERIAL AND SOIL

Parent material refers to the type of bedrock from which the basic component of soil is derived. Parent material is determined by the geology of the location. It can be igneous, sedimentary or metamorphic. Igneous rocks result from volcanic action. Sedimentary rocks are formed as a result of a process known as weathering. Weathering is the physical and chemical alteration of rocks and minerals near the surface of the earth. Metamorphic rocks are igneous or sedimentary rocks that have undergone change as a result of high temperatures and pressure deep underground.

Parent material combines with other state factors; climate, topography, time and living organisms influence soil development. This interaction is depicted in Figure 3.3.

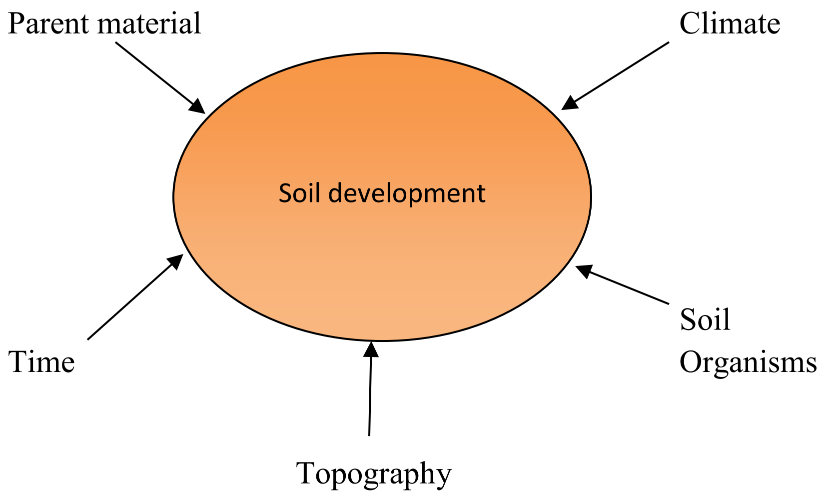


Figure 3.3: Factors influencing soil development

Soil is a crucial to ecosystem functioning. It is the surface on which plants grow in terrestrial ecosystems. It is also the major reservoir for both organic and inorganic chemicals during biogeochemical cycling. Soil is a multiphasic system and consists of solids, liquids and gases. Physical and chemical characteristics of soil have strong influences on the functioning of not only terrestrial ecosystems but on the aquatic ecosystems with which they are linked. Soil not only provides anchorage for plants, it is also the source of nutrients to plants and to soil microbial and invertebrate communities responsible for essential ecosystem services such as decomposition. In terrestrial ecosystems, soil is the primary location for the intersection of geological and biological processes. Soil has three major components. These are the weathered fragments of the parent rock. These fragments usually exist in the soil in various stages of breakdown. The other major components of soil are water and the minerals and organic substances originating from the decomposition of dead organisms. The decomposition of organic matter as a result of microbial action produces a finely ground organic material known as humus. The organic matter content of soil is a very important property that has a direct effect on ecosystem functioning. The optimal humus content for plant growth is about 8%. Soils with less than 1% humus content are regarded as humus-poor.

A key characteristic of soil is vertical structure. Vertical structure of soil also referred to as the soil profile results because soil forming processes such as leaf litter fall happens from top down. Figure 3.4 shows a typical soil profile

O horizon: organic debris, partially decomposed

A horizon: surface horizon, dark colored soil with high mineral and organic content; sometimes with E or eluviation layer

B horizon: subsoil; iron, aluminum, clay, or organic material washed from A horizon may be deposited here

C horizon: substratum; weathered parent material from bedrock

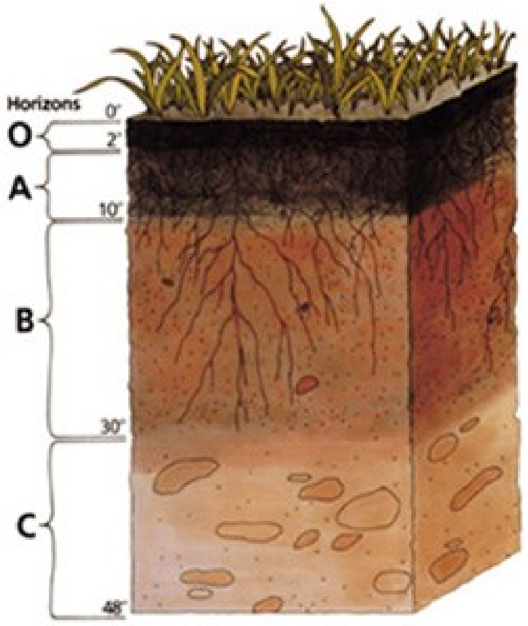


Figure 3.4: A typical soil profile

Five main layers or horizons of soil are recognized by soil scientists. The these layers are designated with letters O, A, E, B and C. The O horizon is made of organic material and is further classified into Oi, Oe and Oa. Oi is made up mostly of undecomposed and slightly decomposed material which is mostly leaf litter, broken twigs and dead bodies or parts of animals. The Oe layer comprises of moderately decomposed organic material while the Oa layer comprises of highly decomposed organic material. Immediately beneath the O horizon is the A horizon which the topmost mineral horizon. It is also where most plant roots are located. Humus is added to this layer making it dark but not as dark as the O layer. The layer just below the A layer is referred to as the E horizon. It is the zone of eluviation or maximum leaching. Most leaching of silicate clays, iron and aluminum oxides takes place in the E horizon. Below the E horizon is the zone of accumulation of iron and aluminum called the B horizon. The lowest zone, which comes just below the B horizon, is the C horizon. It is generally made of slightly weathered and unweathered bedrock material. Below the C horizon is the regolith or bedrock.

Soils vary in their properties from one location to another. This variation reflects the variations in parent material, climate, age and other variables that interact during soil development. Soil properties are important to ecosystem functioning because they modulate availability of nutrients and water to plants. Some important properties of soil are soil texture, soil structure, water-holding capacity, redox potential and soil organic matter content. Other important characteristics are bulk density and cation exchange capacity.

Soil texture

Soil texture is the relative proportion in which different soil particles are represented in soil. Three major categories of particle size are used in soil texture classification. These are clay (less than 0.002mm), silt (0.002 – 0.05mm) and sand (0.05 to 2.00mm). Soil in which a large proportion is represented by more than one of the above categories is referred to as loam or loamy soil. Particle sizes larger than 2mm are referred to as rock or gravel. The major soil textural classes are shown in Figure 3.5. Soil texture is an important ecological factor because it determines the total surface area in a volume of soil. This has implications on water and nutrient availability to plants and soil-dwelling organisms. A matrix of fine-grained particles results in greater surface area to volume ratio. Consequently, fine-grained soils tend to hold more water and nutrients than large-grained soils. Soil texture not only affects water-holding capacity, it also affects other soil properties such as bulk density, nutrient content and redox potential.

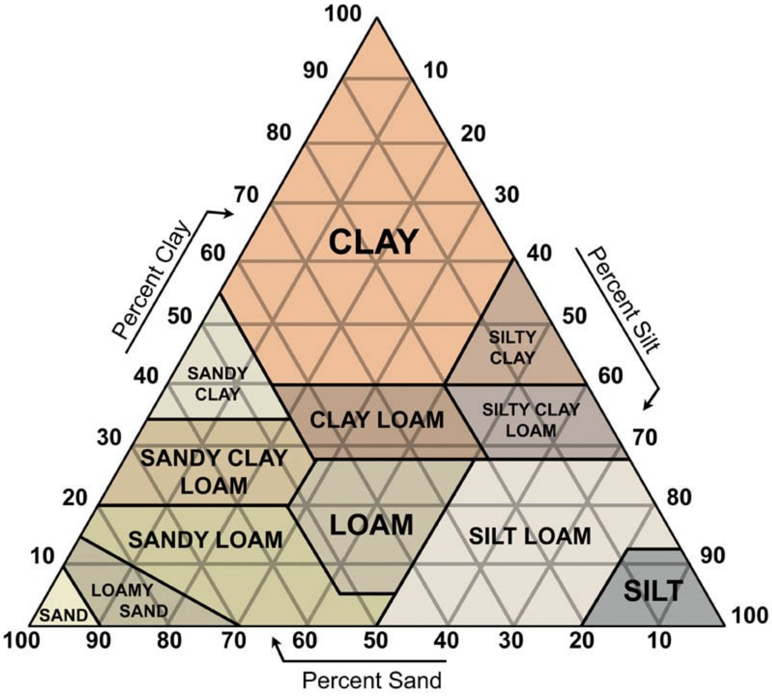


Figure 3.5: Soil textural classes

Soil structure

Many substances found in soil can cement soil particles. Some of these substances include clays, silica, iron oxides and organic matter. Cemented soil forms aggregates when they crack. It is the nature of these aggregates that determines the structure of soil. Soil texture is an important determinant of soil structure. Loam and clay tend to form aggregates much more readily than sandy soils. Soil organisms also play a key role in soil aggregation. Plant roots exudates containing polysaccharides for example act as very potent soil cementing agents. Also, the activities of earthworms, termites, fungi and other organisms help to promote soil particle aggregation. Aggregation, on its part, affects the types of organisms that inhabit soil. For example, cemented soil particles can create anaerobic microhabitats within soil making it possible anaerobic for microorganisms to thrive and to undertake anaerobic biochemical reactions with implications on nutrient cycling.

Water-holding capacity

The water-holding capacity of soil is an ecologically important soil characteristic. It plays a key role in determining the availability of water to plants and to soil organisms responsible for essential ecological processes such as decomposition and nutrient absorption. Water-holding capacity is determined from two parameters namely: field capacity and permanent wilting point.
When soil receives water, at a higher rate than drains out, it ultimately becomes water-saturated. Water drains out of water-saturated soil through a process known as saturated flow. Saturated flow continues until a stage is reached when water can no longer drain out of the soil because the adhesive forces holding water in films on particles equals the gravitational force draining the water away. This point is referred to as the field capacity. Below field capacity, water drains away through the process of unsaturated flow. Unsaturated flow is driven by gradients of water potential within the soil. At a certain minimal water potential, plant roots become unable to remove water from soil particle surfaces. This point is known as the permanent wilting point. The water-holding capacity of soil is the difference between field capacity and permanent wilting point.

Water-holding capacity is affected by both the texture and the structure of soil. For example, the large surface area to volume ratio of clay and organic matter means that soil with a high proportion of these components tends to have higher water-holding capacity.

Redox potential

Redox potential of soil is the electrical potential to loss or gain electrons from chemical reactions taking place in it. Redox potential affects the microbial biota of soil because soil microorganisms derive their energy through oxidation-reduction (or redox) reactions. These reactions involve the transfer of electrons from one reactant to another during which process chemical energy is released for use by the organisms involved. The types of redox reactions that take place in soil are determined by the soil redox potential. Under aerobic conditions oxygen is usually the electron acceptor. Aerobic reactions in which oxygen is the electron acceptor yield the greatest amount of energy. In situations where oxygen is not available (i.e. under anaerobic conditions) alternative electron acceptors have to be used. Absence of oxygen therefore gives advantage to microorganisms that can use alternative electron acceptors. For example, denitrifying bacteria use nitrate as electron acceptor and therefore thrive in the absence of oxygen while aerobic microorganisms are excluded under such conditions. Other electron acceptors include Manganese, Iron, Sulphate, Carbon dioxide and Hydrogen.

Organic matter content

Soil organic matter is the most important reservoir of nutrients used by plants and by soil organisms. It is also a determinant of other characteristics of soil such its water-holding capacity and its structure. All these factors combine to affect nutrient cycling, retention and availability within the ecosystem.

3.4 TOPOGRAPHY

Topography controls the redistribution of materials through the effect of gravitational force and through its effect on the differential distribution of solar radiation and wind deflection at the landscape level. These factors interact with vegetation cover to create local microclimatic conditions with consequences on ecological processes. Gravitational force causes water to move downhill carrying nutrients and particulate matter. It also causes soil to move, leading to the transfer of materials from one location to another within the landscape. Movement of materials in this way affects both terrestrial and aquatic ecosystems.

Another way in which materials can move from one ecosystem to another is as a result of gravity is through the process of erosion. Downhill soil erosion moves particulate materials from one ecosystem and deposits it in another. Topography is therefore a very important influence on the movement of nutrients, organic matter and pollutants between ecosystems.

3.5 TIME

Time is a state factor because change happens in stages. The stages of change can be viewed over geological and evolutionary time or over shorter spans. At geological and evolutionary scale the effect of time on ecosystem function and structure is through parent material from which soil development occurs and through the evolution of organisms. For example, the cycle of rock formation and weathering (the rock cycle) operates over billions of years and governs the distribution of geological materials on the earth’s surface. It is this cycle that produces soil minerals. These minerals not only serve to buffer acidity produced as a result of biological action in the soil but are also the sources of nutrients required for life. Over evolutionary time, natural selection serves to determine the adaptations of organisms and therefore the type of biota that exist in any given ecosystem. The way that evolutionary time can influence ecosystem structure and function can be illustrated with its relationship to species diversity as postulated in the Species-Time hypothesis. According to this hypothesis, communities gain species as they age. Several variations of this hypothesis are in existence. According to one of these variations, younger communities will contain fewer species since they have had less time for species immigrations into them. Based on this argument, the lower species diversity in temperate communities, as compared to tropical ones, is attributable to the fact that they are younger as a result of the last glaciation. Another variation, known as the evolutionary speed hypothesis, argues that higher species diversity in the tropical environments is attributable to the faster pace of evolution in the Tropics as a result of higher ambient temperatures, shorter generation times and increased rates of mutation.

Over shorter time-scales the role of time is through legacies of disturbance and the consequent successional changes that are associated with them. These phenomena are explored further in Chapter 6.

3.6 POTENTIAL BIOTA

The potential biota that of an ecosystem are all the species that can establish themselves, survive and reproduce successfully in an ecosystem. It is from this subset that the biotic community of an ecosystem is drawn.

A key question linked to the role of potential biota as an ecosystem state factor is the how species are recruited into ecosystems and how they are able to establish themselves successfully. Barriers to successful establishment in an ecosystem include dispersal as well as adverse effects of the biotic environment (such as competition, predation and disease) and the abiotic environmental conditions of the environment. This is closely related to the question of why some ecosystems have higher species diversity than others.

One way to test whether a species is capable of existing where it is not found is to conduct a transplant experiment. Transplant experiments involve the deliberate human dispersal of species propagules to locations of interest and must be carefully controlled to prevent undesirable spread of the species under investigation. Transplant experiments show that species found in specific ecosystems are not the only ones that could possibly exist in them. Many species are restricted to the regions where they currently exist simply because of a lack of opportunity to disperse to other regions. Vivid examples of this can be seen from the tremendous success of the European rabbit in Australia after it was introduced there. Another example is the success of Eucalyptus (a tree native only to Australia) in many tropical and sub-tropical regions across the world.

Several hypotheses have been suggested to explain why some environments are able to maintain higher species diversity than others. These include the species-time hypothesis already mentioned in the last sub-section. Others are Species-Area hypothesis, Species-Energy hypothesis, the Intermediate Disturbance hypothesis and the Janzen-Connell hypothesis.

These hypotheses are discussed in Chapter 6 on the control of ecosystem processes.

Chapter 4: Biotic Mechanisms in Ecosystems

4.1 INTRODUCTION

Although the potential biota that can occupy an ecosystem is regarded as a state factor, ecosystem functioning is only affected by the species that have actually colonized and established themselves in an ecosystem. Ecologists tend to approach the study of ecosystems from the perspective of what happens to the biotic component. This is the knowledge needed, for example, to make decisions for the management of natural resources in a sustainable manner. However, to understand what happens to the biotic component, ecologists must also understand how the biotic component affects the abiotic component.

At the ecosystem level ecologists are primarily interested in the effects of abiotic environment on community characteristics and mechanisms. Since communities are assemblages of populations of different species, the primary community-level mechanisms are the interactions that occur between these different species. It is these interactions that drive ecosystem function and determine the characteristics and properties of the community such as its species composition and abundance, its stability and its resilience to disturbance episodes. Abiotic factors serve primarily as the modulators of the outcomes of biotic interactions and eventually on the characteristics and properties of biotic communities. In the next sections of this chapter, we briefly review the main types of biotic interactions within communities, the emergent characteristics and properties of communities and the key concepts and hypotheses related to them.

4.2 SPECIES INTERACTIONS

Interactions that occur between organisms of the same and different species in a community are referred to as biotic interactions. These include trophic interactions such as predation, herbivory, parasitism and disease as well non-trophic ones such a competition (which is exploitative) and mutualism (which is symbiotic and facilitative). In this section we review each one of these types of interactions and some key concepts and hypotheses relating to it.

The study of biotic interactions constitutes the transition between population ecology and community ecology. Population ecologists are interested in how these interactions affect population dynamics. Community and systems ecologists, on the other hand, are particularly interested in interspecific biotic interactions and how these affect community structure and function. Knowledge of interspecific interactions, particularly trophic relationships, provides the framework, in the form of food webs, through which the study of how energy and matter move from one trophic level to another can be undertaken. Interspecific interactions also play a significant role in determining the presence, absence and abundance of organisms in specific environments. This in turn determines how organisms in any specific habitat obtain and utilize energy and nutrients. For example, the presence of trees in a particular location will have profound effects on the surrounding abiotic conditions. The temperature, light intensity and moisture content under the tree canopies will be different from what obtains where there is no tree cover. This will no doubt have implications for the both the litter and soil fauna and flora in areas with tree cover.

Most textbooks of ecology classify biotic interactions in terms of whether they are harmful, beneficial or neutral to one or both of the interacting species. Within that framework, competition, predation, herbivory, parasitism and disease are harmful to one species and beneficial to the other. Mutualism is beneficial to both species while in commensalism neither of the interacting species benefits or loses. In amensalism, one of the species benefits without any apparent loss to the other.

In this book we view interactions from the ecosystem perspective. In other words, biotic interactions are viewed from how they relate to energy flow and nutrient cycling within the biotic community and between it and the physical environment in which it is embedded. Hence interactions are classified as either trophic or non-trophic. Trophic interactions are the direct feeding relationships. These are predation, herbivory, parasitism and disease. Non-trophic interactions are competition and mutualism. Both competition and mutualism affect nutrient cycling and energy transfer through their effects on the ability of organisms to obtain food and other resources that are needed for survival and reproduction. Mutualism facilitates the organism's feeding, survival and reproductive abilities while competition is a constraint on them. In the rest of this chapter we briefly review each of these categories of interactions and some concepts and hypotheses that relate to them.

4.2.1 Predation

Predation refers to the consumption of one organism by another of a different species. The consumed organism is referred to as the prey while the consumer is the predator. Many ecologists distinguish between true predation and herbivory. In true predation the predator kills the prey either before consumption or during the process. In this book we will follow the convention and therefore in this section we use the word predation to refer to what some authors refer to as true predation.

Predation has a great influence in the structure of biotic communities and therefore is a major factor in ecosystem dynamics. Predation influences the distribution, abundance and structure of prey and predator populations. One of the key influences of predation on community structure has been through the evolution of a wide range of anti-predator adaptations by potential prey. The other is that the introduction or removal of a predator into an ecosystem can lead to major changes in community structure and the dynamics of the affected system. A third significant aspect of investigation of predation relates to heterogeneity of habitat in which it takes place. Studies have shown that heterogeneous environments that contain escape spaces or refuges for prey are crucial to the persistence of prey and therefore have a profound effect on the dynamics of predator-prey systems.

Some of the key concepts and hypotheses associated with predation include the keystone species concept and the trophic cascade hypothesis. These are covered in more detail in Chapter 6.

Prey Adaptations against Predation

Animals have developed a wide range of adaptations that help them against predation. Some of the defenses used by animals against predation include chemical defenses, physical defenses, mimicry, cryptic coloration, predator satiation and intimidation.

A rather dramatic display of chemical defense is that exhibited by the bombardier beetle *Stenaptinus insignis*. This species of beetle, which is appropriately named, literally uses chemicals (hydroxide peroxide and hydroquinone) stored in reservoirs its abdomen to produce a bomb for use against the predator (Eisener and Aneshansley, 1982). At the threat of predation the beetles eject the chemicals into a chamber in which they react and are then ejected violently in the direction of the potential predator. Not all chemical defenses are however, as dramatic as that. Many organisms including amphibians, insects and other invertebrates simply produce exudates that repel the potential predator.

Another way in which animals prevent themselves from being eaten by a predator is through coloration. Aposematic or warning coloration is when an animal displays colors that the predator associates with unpleasantness or unpalatability. Bright red colors are usually associated with the presence of toxic chemicals. Toxic chemicals within animals can be manufactured by them through their own metabolic processes. In some instances, however, these toxins are amassed by the prey from the plants or other sources through consumption. For example, the caterpillars of monarch butterflies feed on milkweed plants and through this process accumulate cardiac glycosides that cause emesis in predators that consume them. Monarch butterflies, which also accumulate cardiac glycosides in their tissues, are colored bright orange and black to dissuade potential predators from eating them.

Closely related to coloration is the phenomenon of mimicry. Many animal species show resemblance to another species in an attempt to prevent predation against them. The species showing resemblance is referred to as the mimic while the species that it is a mimic to is called the model. When the model is unpalatable and the mimic is palatable this type of mimicry is called Batesian mimicry. Sometimes, however, many different noxious species converge in color pattern thereby reinforcing the noxiousness of that pattern. In this latter case, mimicry is said to be Mullerian.

In many species coloration is used in a different way than in mimicry. Many species have colors that make it difficult for the predator to detect them in the environment. This type of coloration is known as cryptic coloration. In cryptic coloration the animal adopts colors that blend with the background in the environment

Finally, many animal species reduce the effect of predation on their populations by using a life history strategy known as predator satiation. In predator satiation members of a population synchronize their reproductive cycle so that the progeny are all produced at same time. Since the predator can only eat a certain number of prey at any given time, the probability of being eaten is drastically reduced for each prey. Furthermore, the total number of prey consumed per population is much lower than it would have been if reproduction was not synchronous.

4.2.2 Herbivory

Herbivory is the feeding relationship in which an organism (usually an animal) feeds on a plant or algae. Many ecologists regard herbivory as a type of predation with the predator being the animal and the prey as of the plant or algae consumed. Treating herbivory as a form of predation is particularly useful when using mathematical models to study herbivory.

Herbivory, however, has certain distinct characteristics that separate it from true predation. For instance, true predation (as described in the previous sub-section) is usually lethal to the prey. In the case of herbivory, consumption of the prey is not lethal in itself although in some instances it may ultimately lead to prey death due to a secondary reason (such as disease or physiological failure due to mechanical damage).

Herbivory is exhibited by a wide range of animal taxa. Many vertebrate species are herbivores. Similarly, hundreds of thousands of insect species exhibit one form of herbivory or another. As previously mentioned, herbivory is sometimes intertwined with disease. For example, stem borers are herbivorous insects that feed on the stems of many plants. Stem borer infestation of agricultural crops are treated as a disease by agriculturalists. Another example can be seen in the situation where flies, aphids or wasps sometimes lay their eggs on stems or leaf buds and in so doing induce tumor-like growths known as gall on the infested plants. The larvae of these insects then remains and feeds inside the developing gall where it is protected from predation.

Herbivores are can be classified on the bases of the parts of the plant on which they feed. Frugivores feed on fruit, folivores feed on leaves, nectarivores feed on nectar, granivores feed on seeds. Many species of insects feed on only one plant species and are therefore said to be monophagous. Herbivores that feed on a wide variety of plant species are referred to as polyphagous herbivores.

Plant defenses against herbivores

Plant defenses against herbivory can be classified into two major categories. Defenses that are always present are known as constitutive defenses while those that are switched on when needed are referred to as induced defenses.

Plants use a wide variety of strategies to defend themselves against herbivores. Some of these defenses include the use of morphological features such as thorns and sticky hairs. Thorns are effective against large vertebrate herbivores but not against invertebrate herbivores. To defend against invertebrate herbivores, many plants produce sticky resins that make it difficult to feed on them. Some plants produce trichomes that trap and kill insects.

Some plants use chemical defenses to protect them from herbivores. Chemicals used by plants include alkaloids, phenolics and terpenoids. These chemicals are secondary metabolites produced as part of the primary metabolism of plants. Secondary metabolites usually have a bad smell, taste bitter and are toxic. They therefore serve as an effective deterrent to herbivores. Chemical defenses vary in the quantity of material that a herbivore needs to consume before they become effective as deterrent. On this basis, they can be classified into two major categories. Substances that must be consumed in large quantities before they become effective are known as quantitative defenses while those that are effective at low doses are referred to as qualitative defenses. A key question is why some defenses are qualitative while others are quantitative. This question arises because energetic studies have shown that plants do incur a cost in the production of secondary metabolites. If that is the case, why do plants bother to have quantitative defenses (since a qualitative defense strategy requires the production of only small quantities of the needed substance with presumably less cost to the plant)? Empirical studies have revealed that plants that have relatively long life spans (such as trees and shrubs) tend to possess quantitative defense substances while those with short life spans (e.g. weeds) tend to have qualitative defenses. Plants (such as trees) which are large, easily seen and long-lived are referred to as apparent plants. Plants, such as weeds, that are short-lived, small and difficult to find are referred to as unapparent plants. Why should quantitative defenses dominate in apparent plants while qualitative defenses are dominant in unapparent plants? From evolutionary theory it is expected that species should adopt strategies that best enhance their chances of survival and reproduction. From this perspective, it is expected that qualitative defenses would be the best strategy for unapparent plants since they are not easily found or their life-spans are not long enough for quantitative defenses to take effect. Similar the most effective strategy for apparent plants is to distribute defensive chemicals all over the large bodies to increase its chances of being consumed. As a result, only small amounts of the deterrent can be present in tissue making them only effective after consumption in large quantities. The relationship between plant life-history and chemical defense allocation is an interesting area of ecological research which is likely to continue to retain the interest of ecologists for a long time to come.

Life-history is not the only potential explanation in variation in chemical defense strategy in plants. Other hypotheses include the optimal defense hypothesis and the carbon-nitrogen hypothesis.

The optimal defense hypothesis argues suggests that the different parts of a plant are not equally important to the survival, growth and reproduction of the plant. As result, chemical defenses, which are costly to produce, should be deployed to the parts of the plant that need the most protection. Based on this hypothesis, it is expected that seeds and flowers which are not easily replaced should contain more defenses than leaves and twigs

The Carbon-Nitrogen hypothesis, on the other hand, suggests that carbon and nitrogen (which are important to both growth and secondary metabolite production) will only be allocated to secondary metabolite production after the requirements for growth are sufficiently met. To test this hypothesis it is expected that plants growing in environments with high nitrogen and low carbon availability will tend to have nitrogen-based chemical defenses dominating while those growing in environments with high carbon and low nitrogen availability will have carbon-based substances as dominant defenses.

Apart from quantitative and qualitative noxious or toxic substances, plants have other ways of using chemicals to defend against herbivores. Some plants are able to volatile organic compounds that attract predators that feed on insect herbivores that attack them. Consuelo De Moraes *et al* (1998) studied relationship between damage caused to tobacco plants by the tobacco budworm *Heliothis virescens* and the frequency of visits by the parasitic wasp (for which it is the host) *Cardiochiles nigriceps* to tobacco plants. Their study showed that significantly higher visits were made by the wasp to the damaged plants than to undamaged plants. They also found that damaged plants produced a volatile compound which was not produced by undamaged plants. What was attracting the wasps to the damaged tobacco plants? Was it the smell of the budworm caterpillar larvae, the damaged leaves or the volatile compounds that the damaged plants were producing? To test this, they removed caterpillars and damaged leaves from experimental plants then measured visits by the wasps and compared this to the control treatment (the undamaged plants). Their study showed that, even with damaged leaves and caterpillars removed, wasps' visits to damaged plants were still significantly higher than to undamaged plants suggesting that the wasps were being attracted by volatile compounds that damaged plants produced. When they repeated the experiment with another insect herbivore *Heliothis zea* the maize earworm (which was not the host of C. nigriceps), the number of visits to *H. zea* damaged plants was slightly higher than those of the undamaged plants but much lower than those with *H. virescens* damage. It appears, therefore, that plants are able to produce volatile compounds specifically targeted towards the right type of predator, parasite or disease for the insect herbivore responsible for the damage.

Another very interesting defensive mechanism discovered by field biologists is the mimicry of semiochemicals by plants. Semiochemicals are a group of chemical messengers that alter the behavior of many insect herbivores. They are a major area of research interest for chemical ecologists. Ecdysteroids are an example of semiochemicals. Ecdysteroids stimulate molting in insects. Some plants produce ecdysteroid-like compounds which deceive the insect herbivore to begin molting prematurely thereby causing their death or making them sterile. The end result in either case is that a reduction in the population of the herbivore species affected.

Other types of strategies used by plants to defend themselves against herbivory include mutualism, associational resistance, and selective leaf abscission. An example of the employment of mutualism for plant defense can be seen in the case Acacias and ants. Many species of acacias enter into a mutualistic relationship in which the ants get habitable space on the plants in return for defending the plant against herbivores. Associational resistance is the situation where palatable plants place themselves in locations dominated by unpalatable species making them less accessible to herbivores. Selective abscission is the situation where plants selectively abscise leaves that are highly infested with invertebrate herbivores and in so doing drop them to the ground where they have no access to the plant.

Despite the wide range of defenses exhibited by plants, herbivores are still able to have a strong impact on the population densities. The strategies used by herbivores are wide-ranging and include mechanical and behavioral adaptations, host manipulation, symbiosis with microorganisms and the possession of digestive enzymes that can counter the effects of secondary metabolites.

Concepts and Hypotheses on Herbivory

Herbivory plays a key role in determining the structure and dynamics of communities and has therefore been a prominent area of ecological research. Many studies of herbivory are centered around three major themes. These are:

(i) The nature of plant defenses against herbivory
(ii) The impact of herbivores on ecosystem processes such as primary production.
(iii) The effect of plants on herbivores

Some of the measure hypotheses associated with herbivory include, intermediate disturbance hypothesis and the green world hypothesis. These are reviewed in more detail in Chapters 5 and 6.

4.2.3 Parasitism and Disease

Parasitism is a situation when one organism feeds on another without directly killing it in the process. Some authorities regard parasitism as a form predator-prey relationship similar to the situation in herbivory. Like herbivory, but unlike true predation, parasitism in most cases is not lethal to the prey. The exception to this is rule is found in a specific type of parasitism in which the parasites are referred to as parasitoids. Parasitoids are usually lethal to their hosts. In parasitism the prey is referred to as the host while the predator is the parasite. Another difference between parasitism and both herbivory and true predation is that in the former two cases the prey is usually smaller than the predator. In parasitism the host is very often much larger than the parasite.

Host-parasite relationships play a crucial role in the determination of the structure of biotic communities. Several aspects of parasitism are of specific interest to ecologists. The first of these is the wide range of attributes and lifestyles exhibited by parasites. Secondly, ecologists are interested in the wide range of defenses that hosts possess against parasites that threaten them. A third ecologically significant fact about parasites is their ability to cause high mortality in host populations thereby potentially altering the structure of biotic communities. In the rest of this section we take a look at each of these ecological aspects of parasitism. In the rest of this section we review some of the empirical and theoretical findings relating to the ecology of parasitism and some of the major hypotheses put forward to investigate them

Attributes and Lifestyles of Parasites

Parasites are found in a wide range of taxa and show many different morphological and life-history variations. On the basis of size, parasites can be classified as being either microparasites or macroparasites. Microparasites are microscopic and are not easily seen without the use of some form of magnification. Microparasitism is usually associated with disease. Disease-causing bacteria and protozoa fall into this category of parasites. Transfer of microparasites may occur directly or through a vector such as an insect. Macroparasites, on the other hand, are relatively large and can be seen without magnification. They also, usually, have a long generation time unlike microparasites. Many macroparasites live their lives in one or more hosts but release their juvenile stages outside the body of the host. Parasites can also be classified on the basis of whether they live inside or on the outside surfaces of the host. Endoparasites reside inside their hosts while ectoparasites attach themselves to the outside surfaces of the host

Most parasites are able to live off the host for very long periods without killing it. The exception to this is a group of parasites known as parasitoids. Parasitoids, which are mostly insects, invariably lead to the death of their host. The adult parasitoid lays its eggs in or on the host after which the larvae develop inside the host. By doing this the parasitoid uses the host as the source of nutrients and energy for development of its offspring killing the host in the process. Parasitoids have been subjects of tremendous amounts of research because of their potential as biological pest control agents

Another type of parasitism is known as kleptoparasitism. Kleptoparasites steal their hosts resources. A good example of this type of parasitism is the brood parasitism that occurs in birds. Many bird species such as whydahs, cowbirds and cuckoos manipulate the host species into taking care of their young for them. One way they do this is to lay eggs that look almost exactly like those of their host and then to place them in the nests of their hosts. The host then incubates their eggs for them and raises their nestlings.

The wide range of attributes and life-histories of parasites is a key area of ecological research interests. Ecologists are interested in the implications of such variation on community dynamics and ultimately on the ecosystem itself.

Host species of parasites have also developed a wide range of adaptations to survive the effects of parasitism. These defenses play a key role in sustaining host populations despite the pressures of parasitism. A notable observation from empirical studies is that in spite of defenses mounted by host populations, parasites can sometimes devastating levels of mortality on them. The circumstances under which this happens are of great interest to ecologists. Studies of the effects of parasites on community structure usually involve the removal of parasites from the community being studied. Parasite removal experiments show that native parasites do have strong effects on native host populations. The studies also show that invasive species may be even more devastating to host populations than native species

Impacts of Parasitism and Disease

Empirical studies show that parasitism and disease can profoundly influence the populations of host populations. This is the knowledge behind the use of biological control programs which use parasites or pathogens to control for the control invasive species. A much cited example is the case of the prickly pear *Opuntia stricta* and the moth *Cactoblastis cactorum*. In the 1800s, *O. stricta,* which is native to North America was introduced into Australia as an ornamental plant. It later escaped into the wild and by the 1920s was covering over 20 million hectares of land. In its native North America, the spread of *O. stricta* was restricted whereas in Australia it found very ideal physical conditions and did not have natural enemies (herbivores, parasites or diseases) that could control its population. A possible way to control the population of *O. stricta* in Australia, therefore, was to introduce one or more of its natural enemies from its native North America. The candidate found for this was the moth *C. cactorum*. The introduction of *C. cactorum* into Australia proved totally effective in the control of *O. stricata*..

C. cactorum was able to decimate populations of *O. stricta* by consuming it and in the process also creating conditions on the cactus that made it possible for disease-causing microbes to inhabit and cause further destruction. This connection between parasitism and disease is widespread in nature and probably accounts for the tremendous success of the control program.

The case of the control of the invasive species *Opuntia* in Australia illustrates how parasites can impact on populations through consumption. However, consumption is not the only way that parasites control population dynamics within ecosystems. Another way that parasites can do this is through the manipulation of the behavior of their hosts.

4.2.4 Mutualism

Mutualism is a facilitative association between two species in which both species benefit. Mutualisms are very essential drivers of ecosystem functioning. Many biotic mechanisms that affect reproductive success such as pollination and seed dispersal are mutualistic. Sometimes neither of the partners in a mutualistic relationship can survive without the other. In that case the relationship is referred as obligate mutualism. An example of obligate mutualism is found in lichens. Lichens are a result of an inseparable complex of fungi and algae. In some mutualisms, each of the partners is able to survive without the other but both do better when they are in alliance. This later type of mutualism is referred to as facultative mutualism. Another way to classify mutualism is to base the categories on the nature of services provided as a result of the relationship. In this scheme, mutualisms that facilitate the dispersal of propagules, such as pollination and seed dispersal are referred to as dispersive mutualisms. Similarly, mutualisms in which one partner defends the other partner in exchange for habitable space or some other resource are referred to as defensive mutualisms. When a mutualism results in both partners having greater access to a resource it is referred to as a resource-based mutualism

4.2.5 Competition

Competition differs from all the other biotic interactions previously described. In competition, unlike the other interactions, competitors reduce each other's capacities to occupy habitats within. Competition therefore affects both participants negatively.

Competition between individual organisms arises because certain resources within the environment inhabited by them are limited in availability. Ecologists refer to this condition as resource limitation. Resource limitation can lead to competition between individuals of the same species as well as those of different species. Competition between individuals of the same species is referred to as intraspecific competition while that between individuals of different species is referred to as interspecific competition. Interspecific competition is a major determinant of the structure of biotic communities and therefore of ecosystem dynamics.

Competition can be classified in many different ways. One way is to look at competition either as an exploitative process or as an interference process. In exploitative competition, organisms compete indirectly by consuming or occupying as much of the resource as possible. The more of the resource taken by one of the competitors the less of it is available to the other competitors. In exploitative competition the efficiency with which individuals or species extract the resource is the key success factor. Competition can sometimes, however, be through interference. In interference competition, a competitor actively tries to prevent co-competitors from having access to the resource. This is done through some form of behavior (such as physical fighting or deception) or by the releasing, into the environment, substances that prevent competitors from having access to the resource. A good example of interference competition is when animals exhibit territorial behavior. This behavior is referred to as territoriality. In territoriality, the animal aggressively defends a territory in which the limited resource is located, thereby preventing competitors from having access to the resource. Some plants, invertebrate animals and bacteria exhibit interference competition by secreting toxic or repellant substances to prevent competitors. This process is known as allelopathy.

Concepts and Hypotheses on Competition

Several concepts and hypotheses have emerged in relation to competition. Some of the major concepts relating to the role of competition in community and ecosystem dynamics are:

(i) Mathematical models can be used to predict outcomes of competition
(ii) Species cannot coexist if they occupy the same niche (The competitive exclusion principle)
(iii) Resource partitioning allows species to coexist
(iv) Competition can have significant evolutionary and ecological influences on a species' niche dimension

In the rest of this sub-section, we briefly examine each of these concepts. Another major concept associated with competition is that its outcome can be influenced by the biotic and abiotic environment in which it takes place. Hence, one competing species may win under a set of environmental circumstances and the reverse may happen in a different environmental setting. The physical conditions (referred to as modulators) within an ecosystem are one of the interactive controls that influence ecosystem processes. Another interactive control that influences ecosystem processes is the biotic community. In chapter 6 we examine how competition outcomes can be influenced by the effects of modulators (the abiotic environment) and the biotic community (other species).

Mathematical modelling of competition

Several arguments have been put forward to explain how competition affects the nature of communities. The framework for these arguments is provided by theoretical models that predict the outcomes of competition. Two of the most prominent models are the Lotka-Volterra model and the Tilman model. The Lotka-Volterra model is the earliest and was first proposed by the American Alfred J. Lotka and the Italian Vito Volterra in the 1920s. A more recent and widely referred to, model is that proposed by the American Ecologist David Tilman (Tilman 1982, 1997). Tilman's model tries to address the main criticism of the Lotka-Volterra model which is that it does not specify the mechanisms that drive the process of competition.

The competitive exclusion principle

The niche of a species is a combination of all the range of conditions in which the species can survive and role of that organism in the community in which it exists. The concept of a niche for each species was first put forward by Joseph Grinnell (Grinnell 1917, 1924). Grinnell's concept of the niche was centered around the influence of the physical environment on the organism. In 1927, however, the British ecologist Charles Elton expanded the definition of the niche to include the interactions of the organism with other organisms as well as the effect of abiotic environment on it. In 1957, the ecologists G. E. Hutchinson provided a much more rigorous definition of ecology in which proposed the theoretical concept of the niche of a species as an n-dimensional hypervolume. In this definition, n stands for all the theoretically possible environmental factors (both biotic and abiotic) that a species can survive and reproduce under. This is the potential niche of the species. In reality, however, the organism is unable to reach this potential since other organisms are restricting it through competition, predation, parasitism, disease and other biotic interactions. The species can therefore only occupy a realized niche in the community in which it exists.

Both the Lotka-Volterra and the Tilman models of competition predict that no two species can occupy the same niche. When species compete strongly, only one of them wins. The other is driven into extinction.

Numerous laboratory and field tests of the Competitive Exclusion Principle (also known as Gause's principle) have been conducted. One of the earliest of these experiments was conducted by the Russian ecologist Georgyi Gause. Gause was able to demonstrate competitive exclusion in the laboratory using several species of paramecium.

4.3 BIOTIC COMMUNITY

In section 3.2 we looked at biotic interactions. Population ecologists tend to study the interactions of two species at a time. We saw that mathematical models such as the Lotka-Volterra model look at just two species at a time. This type of approach simplifies the situation and makes it possible for ecologists to have an idea what could happen. They are said to have a learning or heuristic value. In real life situations, however, biotic interactions involve a complex network of several interactions between many species. Patterns and processes of interactions involving large numbers of species are studied by community ecologists. A community is an association of interacting species inhabiting a defined area. Ecologists may study the insect community associated with a particular tree species or the fish community in a lake or the plant community of a valley, mountain top or floodplains of a river.

Community ecologists seek to understand how various biotic and abiotic aspects of the environment influence the structure of communities. Community structure includes attributes such as the number of species, the relative abundance of species, and the kinds of species comprising a community.

Studying large numbers of species is usually very time-consuming and difficult. Most community ecologists, therefore, work with restricted groups, focusing, for example on communities of plants, mammals, or insects. Some ecologists restrict their focus even more by studying guilds. A guild is a group of organisms that all make their living in a similar way. Examples of guilds include the seed-eating animals in area of desert, the fruit-eating birds in a tropical rainforest, or the filter-feeding invertebrates in a stream. Some guilds consist of closely related species while others are taxonomically heterogeneous. For example, the fruit-eating birds of many South Pacific islands consist mainly of pigeons while the seed-eating guild in the Sonoran Desert includes mammals, birds and ants. The term guild is usually used by animal ecologists. Plant ecologists and botanists prefer to use the term life-form instead of guild. The life-form of a plant is a combination of its structure and its growth dynamics. Like the members of an animal guild, plants of similar life-forms exploit the environment in similar ways.

By studying animal guilds or plant life-forms, ecologists can focus their energies on a manageable and coherent portion of the community

The biotic environment is made up of populations of various species which exist in form of biotic communities. Since ecology is primarily a biological subject, the primary focus in the study of ecosystems is to understand how biotic communities are affected. A biotic community is simply an assemblage of organisms of different species that inhabit and interact in a defined area. For example, one may study the community of macro-invertebrates in a specific soil habitat or the community of birds in a forest. Similarly, one can study the microbial community of the gastro-intestinal tract of a mammal or a community of benthic organisms in a lake or pond. The boundaries of a community are usually defined by the ecologist depending on the specific reason for which the investigation is being conducted. Biotic communities constitute the framework of ecosystems. It is the dynamics of these communities as moderated by their prevailing abiotic environment that determine the nature of any ecosystem. Energy is transferred along the trophic structure and nutrients are cycled essentially as a result of biotic activity. In essence, it is biotic communities that give ecosystems life. They take the energy from the sun and utilize it to cycle nutrients.

Biotic communities exhibit certain emergent characteristics and properties that can only be measured at this level of ecological investigation. Commonly measured characteristics of communities include species richness, species abundance and species diversity. Another commonly measured characteristic of communities is their food web or trophic structure. In the next sections of this chapter, we briefly review these characteristics and present some of the major concepts and hypotheses relating to them.

4.3.1 Species Richness and Abundance

The species richness of a community is the total number of species that exist in that community. Species abundance, on the other hand, is the total number of individuals in the community.

One of the patterns observed in the structure of communities is that most species show a moderate level of abundance. A few species are highly abundant and a few are extremely rare. This observation was first made by Frank Preston (1948). Preston argued that the best way to think of species abundance is in terms of relative abundance. In other words it is more useful to define a species as being twice or three times as abundant as another species than to present absolute abundance. This led Preston to graph the abundance of species in a collection as frequency distributions, where the classes of species abundance were intervals of 1-2, 2-4, 4-8, 8-16, etc. The distributions that Preston obtained are now known to be universal for most collections and are referred to as lognormal distributions. The distribution of “commonness and rarity” among species described by Preston is one of the best documented patterns in natural communities. Although this is the case in general, many regions still remain unexplored to test whether exceptions to this pattern exist under certain circumstances. There is therefore an opportunity for further investigation in this area.

4.3.2 Trophic Structure

The trophic structure of a community refers to the feeding relationships that exist within that community. After primary production by autotrophs, energy and nutrients are transferred across trophic levels in a food chain when one organism feeds on another. Food chains are linked together to produce a food web. Food webs can be diagrammed using arrows to link species according what they eat or what eats them. Many community ecologists specialize in identifying, documenting and studying the dynamics of food webs.

Work on food webs has revealed many characteristics that are common to such webs. One of such characteristics relates to the lengths of the food chains that make up food webs. Such food chains are usually short. Several hypotheses have been put forward to explain why food chains are usually short. Two of the prominent ones are the energetic hypothesis and the dynamic stability hypothesis

Other characteristics of food webs relate to how their structure and dynamics are affected. Perhaps one of the most important findings regarding food webs is that the feeding activities of a few keystone species may control the structure of communities. This property of food webs was first revealed by the ecologists Robert Paine. Another key finding about food webs introduced species can sometimes have very profound effects on them as was the case when a predator The Nile perch (*Lates niloticus*) was introduced into Lake Victoria in East Africa. The Keystone species concept and the role of exotic species on trophic structure are discussed in Chapter 6 (Controls on Ecosystem Processes)

Chapter 5: Ecosystem Processes

5.1.A GENERAL FRAMEWORK

As mentioned in Chapter 3, ecosystems are made up of reservoirs or pools of materials and energy. These pools are linked together into a system by fluxes or flows of nutrients and energy. Hence the two most important ecosystem processes that are of interest to system ecologists are the transfer of energy and the cycling of water and nutrients.

In all ecosystems, movement of nutrients and energy are controlled by the key processes of synthesis, consumption, decomposition and assimilation. The relationship between these primary processes is conceptualized in Figure 5.1.

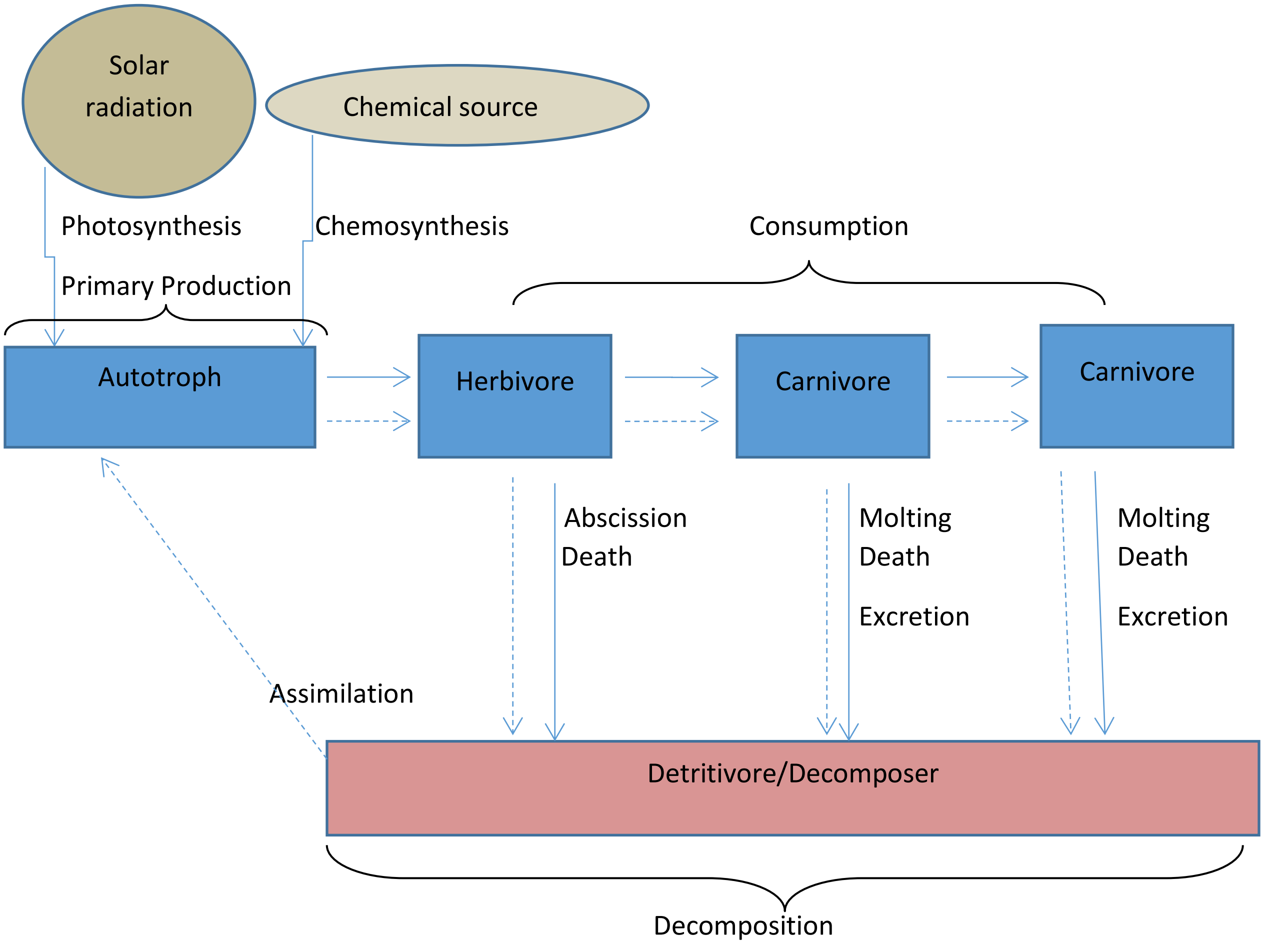


Figure 5.1 Key ecosystem processes and pathway for the transfer of energy (⟶) and nutrient cycling (- - -►)

Synthesis is the process responsible for primary production of biomass by autotrophic organisms. During synthesis energy from solar radiation or a chemical source is harnessed and used to produce biomass. When solar radiation is the source of energy the process is referred to as photosynthesis. Nutrition of organisms through the process of photosynthesis is known as photoautotrophy. Photosynthesis is the most significant form of synthesis of primary biomass on the planet earth. Photosynthesis is, however, not the only mechanism of autotrophic nutrition. Another form of synthesis that can occur is chemosynthesis. In chemosynthesis, the source of energy is usually an inorganic or organic substance. Chemosynthesis carried out by microorganisms living in habitats where solar radiation cannot reach (e.g. deep sea hydrothermal vents). Chemosynthesis driven nutrition is known as chemoautorophy. There are two types of chemoautotrophy. When the energy source is an inorganic chemical, the process is known as chemolithotrophy. When, however, the source of energy is from an organic substance, the process is referred to as chemoorganotrophy. Organisms that obtain energy through autotrophic nutrition are known as autotrophs. Autotrophs are also referred to as primary producers since they are responsible for the primary production of biomass in ecosystems.

Another process that drives the flux of energy and materials through the ecosystem is consumption. Many organisms carry out a type of nutrition known as heterotrophic nutrition. Unlike autotrophic nutrition, heterotrophs (organisms that are heterotrophic) cannot carry out photosynthesis or chemosynthesis. Instead, they obtain their energy and nutrients by feeding on other organisms. Heterotrophic organisms are also known as consumers. Consumers that feed directly on primary consumers (e.g. plants, cyanobacteria and green algae) are referred to as primary consumers. Primary consumers are also known as herbivores since they feed on plant material. Consumers that feed on herbivores are referred to as secondary consumers while those that feed on secondary consumers are referred to as tertiary consumers. This chain of consumption creates food chains in a web of trophic relationships. Trophic relationships within an ecosystem constitute the trophic structure of the communities within the ecosystem.

A third mechanism of material and energy flux within ecosystems is the process of decomposition. Decomposition is actually partly a process of consumption by microorganisms and fungi within the ecosystem. Decomposition is a crucial step in the flux of materials and energy in ecosystems since it is responsible for the breakdown of materials into a form that can be absorbed by autotrophic organisms and hence for the completion of the cycling of nutrients within the system. Decomposition begins with the consumption of detritus (dead organic matter) by organisms known as detritivores. Detritivores are fungi and invertebrate animals such as dung beetles, earthworms and termites that feed on dead organic matter. They break down organic matter and make it more readily available to microbial decomposers in the soil, sediment or water environment.

Finally, once dead or excreted organic materials are decomposed into inorganic substances these become available for absorption either from soil, water, sediment or the atmosphere.

5.2.PRIMARY PRODUCTION AND ENERGY TRANSFER

Primary production is the conversion of inorganic forms of energy into organic forms. The main process through which this takes place is through photosynthesis. Photosynthesis is a carbon fixation process that provides the carbon and energy that drive biological processes within ecosystems. It is the energy fixed through this process that supports primary biomass production through plant growth. Plants are therefore referred to as primary producers. Primary biomass is consumed by herbivores that are themselves consumed by carnivores. Since herbivores are the first in the line of consumers, they are referred to as primary consumers. Carnivores are secondary consumers. Some carnivores feed on other carnivores and are therefore referred to as tertiary consumers. Detritivores, because they mostly feed on dead plant material, tend to be regarded as mainly primary consumers.

The three main elements making up organic matter are carbon, hydrogen and oxygen. Photosynthesis is the process by which carbon enters ecosystems. That is why it is sometimes referred to as carbon fixation. Carbon derived from photosynthesis accounts for nearly half the organic matter on Earth; hydrogen and oxygen make up the remaining.

At the organismal level, photosynthesis is controlled by factors affecting plant physiology such as light, carbon dioxide and nitrogen availability. Light and carbon dioxide are the reactants while nitrogen is the basic element with which the enzymes that drive biochemical reactions are made. Temperature also plays a key role because of its effect on rates of reactions.

At the ecosystem level, the combined primary production by individual autotrophs within the ecosystem totals into a gross primary production (GPP) for the system. The rate at which GPP takes place is known as the rate of primary production. This is measured as the amount of energy fixed over a time interval. Since autotrophs have to use part of primary production to meet their own energetic needs, the productivity of an ecosystem is actually the net primary production (NPP). NPP is the net gain in carbon by vegetation after loss due to plant respiration is subtracted from GPP. Apart from respiration, plants loss carbon through other processes such as litterfall, root exudation and transfers to microbial symbionts. In terrestrial ecosystems, all these losses end up in the soil and therefore account for the organic matter content of soil. Soil organic matter (SOM) is the largest pool of carbon in terrestrial ecosystems. Another way in which plants lose carbon is through herbivory. Herbivory is the main way through which plants lose carbon in aquatic ecosystems. Finally, plants also lose some of the carbon they gained during primary production through combustion when fires break out and through the emission of volatile organic compounds.

As previously mentioned, a substantial part of carbon fixed by primary producers during photosynthesis is transferred to heterotrophic organisms through consumption. The carbon balance of ecosystems, therefore, not only depends on the vegetation balance but also on respiration by heterotrophs. Heterotrophic respiration converts organic matter into carbon dioxide which is then released into the atmosphere where it becomes available for photosynthesis. Carbon dioxide can also be released from organic matter in ecosystems through combustion during fire incidents. In addition, lateral fluxes of carbon leaching and animal movements play critical roles in the movement of carbon between ecosystems.

Several key issues relating to primary production and energy transfer that may be of interest to the research student are worth considering. These include the role of limiting factors such a temperature, moisture and nutrient availability on primary production, the role of consumers on primary production and the efficiency of energy transfer in ecosystems. In the rest of this section we review some of these issues.

5.2.1. Key concepts in primary production and energy transfer:

- At global level, primary production is limited by temperature and moisture in terrestrial ecosystems and by nutrient availability in aquatic ecosystems.
- At the local level, terrestrial primary production may be limited by soil nutrient availability.
- Producers, consumers and decomposers are linked in food chains that combine to form food webs.
- The chain lengths of food chains are usually short.
- Food webs tend to contain some species that have disproportionately large impacts on the ecosystem.

Terrestrial primary production: role of temperature and moisture

The distribution of terrestrial biomes on earth clearly coincides with global patterns of temperature and precipitation. Terrestrial primary production is highest under warm and moist conditions such as those obtained in the tropical forest biome. As mentioned in Chapter 3, terrestrial temperature variation on the surface of the earth is primarily determined by the distribution of solar radiation on the planet. The equatorial region receives the most solar radiation and is therefore the warmest while polar regions receive the least radiation are therefore the coldest. Energy from solar radiation not only determines regional temperature ranges but is also responsible for pressure variations that determine wind and ocean current movements and consequently precipitation across the globe. Thus, the distribution of energy and water, the two main determinants of primary production, are interlinked.

One way to study the relationship between moisture and temperature on primary production in terrestrial ecosystems is to compare the production patterns with annual actual evapotranspiration (AET). AET is the total amount of water that is transpired and evaporated from a specified area over a period of one year. It is measured in millimeters of water per annum.

AET is affected by both temperature and precipitation. Primary production across the surface of the earth is highest in areas where both precipitation and temperature are high. It is low if either temperature or precipitation is low. Consequently, terrestrial primary production is low in hot deserts because precipitation is low there even though temperature is high. Similarly, production is low in the tundra where precipitation can be high but temperature is low.

One of the earliest studies of the relationship between temperature and moisture, and primary production was conducted by Rosenzweig (1968). Rosenzweig's study revealed a positive correlation between net primary production across several ecosystems and the actual evapotranspiration in the same areas (Figure 5.2)

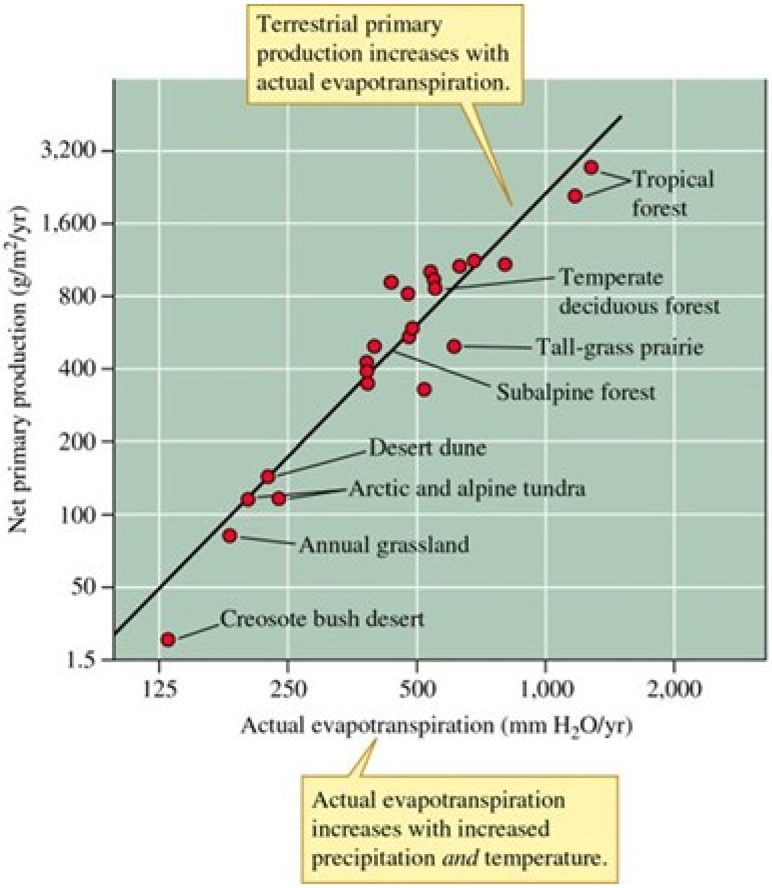


Figure 5.2: Relationship between aboveground primary productivity and actual evapotranspiration (Data from Rosenzweig (1968). Source: Molles, 1999)

Since the study by Michael Rosenzweig, many other studies have been conducted to demonstrate the positive correlation between actual evapotranspiration, precipitation and net primary productivity (for example: Bazilevich *et. al*., 1971, Lieth, 1975, Grier and Running, 1978, Box, 1980, Sala *et. al*., 1988, Lauenroth and Sala, 1992)

Terrestrial primary production: role of soil nutrients

Although there is generally a positive correlation between actual evapotranspiration and primary production, the degree of correlation tends to vary from one location to another. These differences are attributable to local-level variations in soil nutrient availability. Within biomes, therefore, variations in terrestrial primary production are largely attributable to soil fertility. One of the early studies of the role of soil fertility on primary production was by the German chemist Justus von Liebig. Liebig (1840) pointed out the significance of nutrients as limiting factors and in plant growth. He put forward what is now known as Liebig's Law of the Minimum. According this law, a minimum amount of a limiting nutrient has to be present to prevent it from limiting plant production. In other words, a single limiting nutrient can prevent production reaching its potential even if other nutrients are abundantly available.

Modern studies of soil fertility show that Liebig's Law of the Minimum is too simplistic. The studies show that terrestrial production is affected by several interacting factors which of course include limiting nutrients.

Although Liebig was primarily working on agricultural production, ecological studies involving the addition of fertilizer to experimental plots have demonstrated increases in primary production in the experimental ecosystems involved. For example, Shaver and Chapin (1988) conducted experiments in which they added fertilizer containing nitrogen, phosphorus and potassium in a Tundra ecosystem. The study showed that net primary production increased significantly in the experimental plot compared to controls. Increase production was over 20% and as high as 300% in some plots.

Aquatic primary production: the role of nutrient availability

One of the best documented patterns in ecosystem ecology is the relationship between nutrient availability and primary production in aquatic systems. Many studies on this relationship have been conducted. Some of these studies involved the experimental manipulation of a specific nutrient e.g. phosphorus or nitrogen in controlled laboratory studies while others were carried out on whole lake ecosystems. Some of the earliest studies in this area include the Japanese lake studies of Hogetsu and Ichimura, 1954, Ichimura, 1956, Sakamoto 1966. Later, in 1974, Dillon and Rigler published work to show a similar relationship to the Japanese findings between total phosphorus and phytoplankton biomass in Canadian and other temperate lakes. One of the most cited studies in this area is the whole lake ecosystem studies of Findlay and Kasian (1987). The result of this study (summarized Figure 5.3) showed that nutrient additions to a whole lake ecosystem resulted in a drastic increase in phytoplankton biomass production thereby confirming nutrient availability as a significant limiting factor of primary production in aquatic ecosystems.

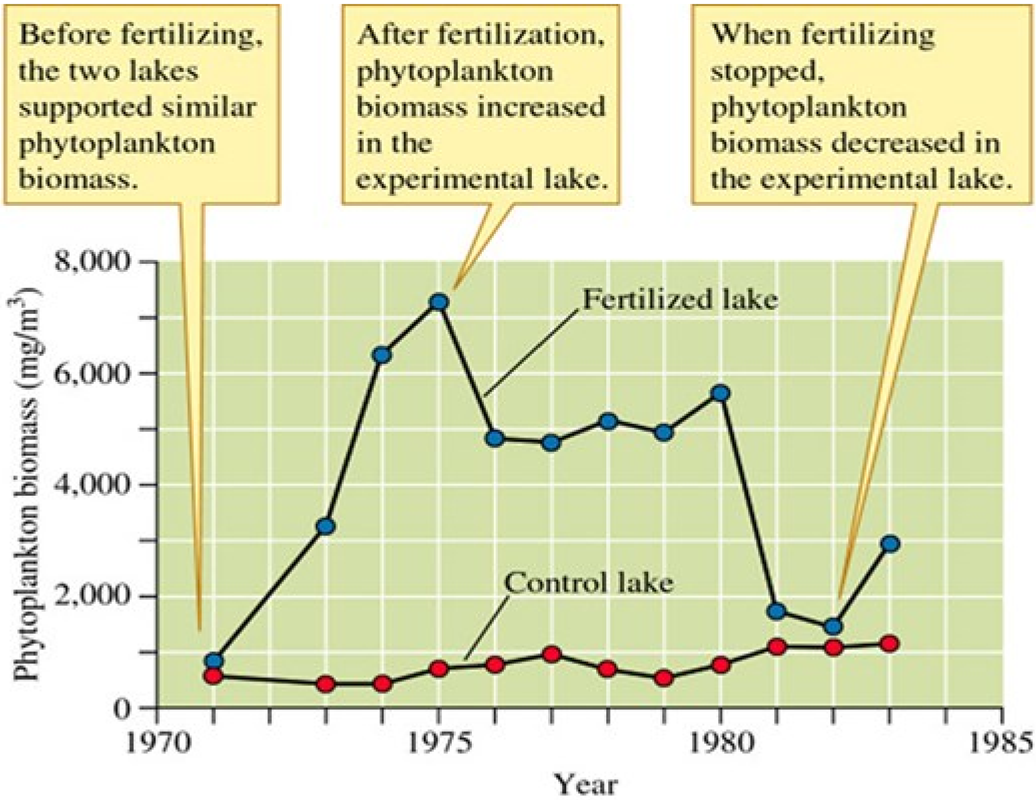


Figure 5.3: Addition of nutrients to a whole lake ecosystem resulted in a drastic in phytoplankton biomass production. (Data from Finlay and Kasian, 1987; Source of Diagram: Molles, 1999)

Primary production: the role of consumers

Another very important concept relating to primary production in both terrestrial and aquatic ecosystems is that consumers can influence the rate of primary production. Earlier in this chapter we referred to the role that nutrients and physical conditions such as temperature can play in primary production. This type of control is referred to as bottom-up. Studies have also shown that controls on primary production can be top-down in some instances. Top-down control is when the trophic role of a consumer leads to effects on primary production. Top-down control is referred to as trophic cascading and is treated in more detail in Chapter 6 on control of ecosystem processes. The hypothesis associated with this concept is the “trophic cascade hypothesis” which is covered in Chapter 6. Top-down control can lead to cascading effects that lead to changes in nutrient availability in aquatic ecosystems. As was mentioned in the previous section, nutrient availability is a key determinant of primary productivity in aquatic ecosystems. Consequently, predation has a great influence on primary production

Another way in which consumers can affect primary production is through the effects of herbivores. One of the most important contributions to this area is the studies of the effects of large herbivores on the ecosystem of the Serengeti National Park in East Africa conducted by Samuel McNaughton. The relationship between intensity of grazing and primary production found by McNaughton (1985) is summarized in Figure 5.4. The study showed that plants under grazing tend to compensate for damage by increasing growth and that at intermediate levels of grazing this actually results in a net increase in biomass. When grazing is absent, growth slows down. Growth is also slowed down by high intensity grazing. This finding is consistent with the Intermediate Disturbance Hypothesis, which is the idea that intermediate disturbance levels enhances the efficiency of ecosystem functioning.

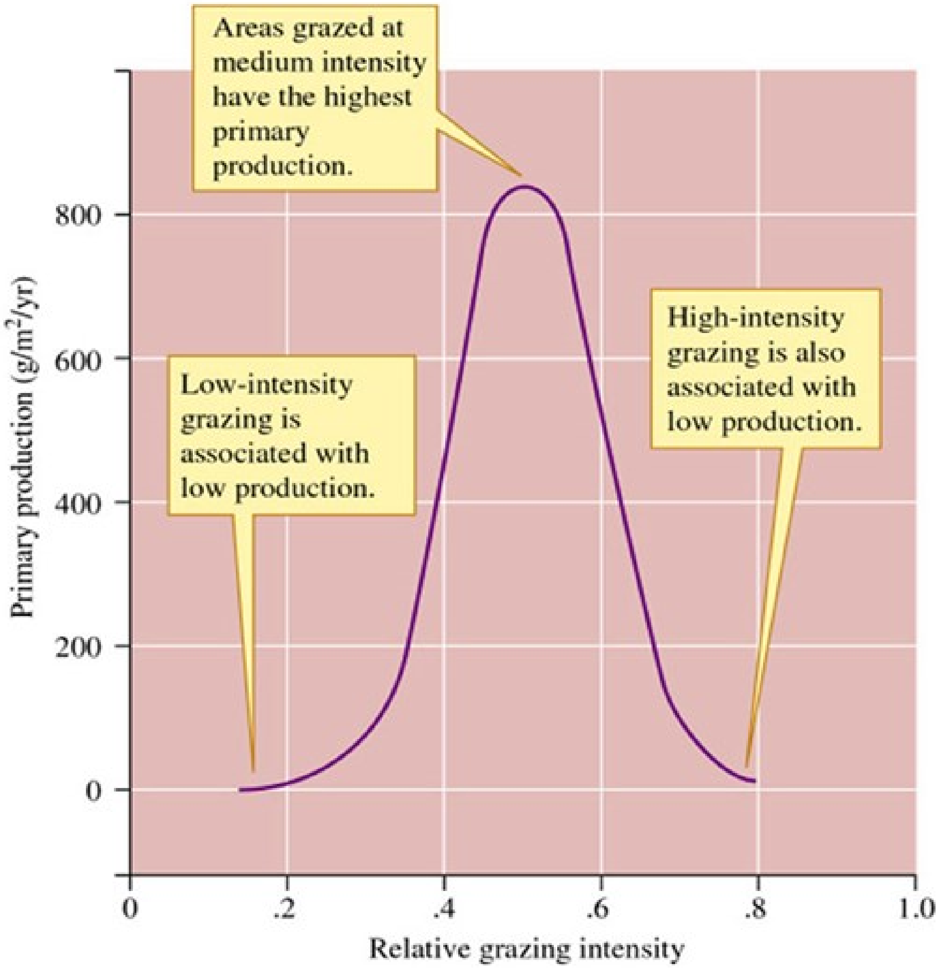


Figure 5.4: Effect of large herbivore grazing intensity on primary production in the Serengeti. (Data: McNaughton, 1985; Source of Diagram: Molles, 1999)

Food Chains and Food Webs

One of the key concepts in the understanding of ecosystems is that of the food web. The structure of food webs, for example, has been extensively studied in relation to ecosystem characteristics such as resilience, stability and ecosystem health.

Food webs are made of food chains joined together. Food chains represent the chain of consumption of one organism by another through which energy and nutrients originating from primary producers reach consumers within the system. Nutrients ultimately cycle back to primary producers through the process of decomposition when they are released into the soil and absorbed and assimilated by plants through their root systems.

Each level in a food chain is known as a trophic level. A key pattern observed in all ecosystems is that food chains tend to be short i.e. the number of trophic levels are limited. The primary explanation for this is that some energy is lost at every level. According the Second Law of Thermodynamics, every time energy is transformed some of it is lost as heat. Thus, nutrients are cycled in ecosystems, but energy is not. It is this inefficiency in food chains that leads to food pyramids (Figure 5.5).

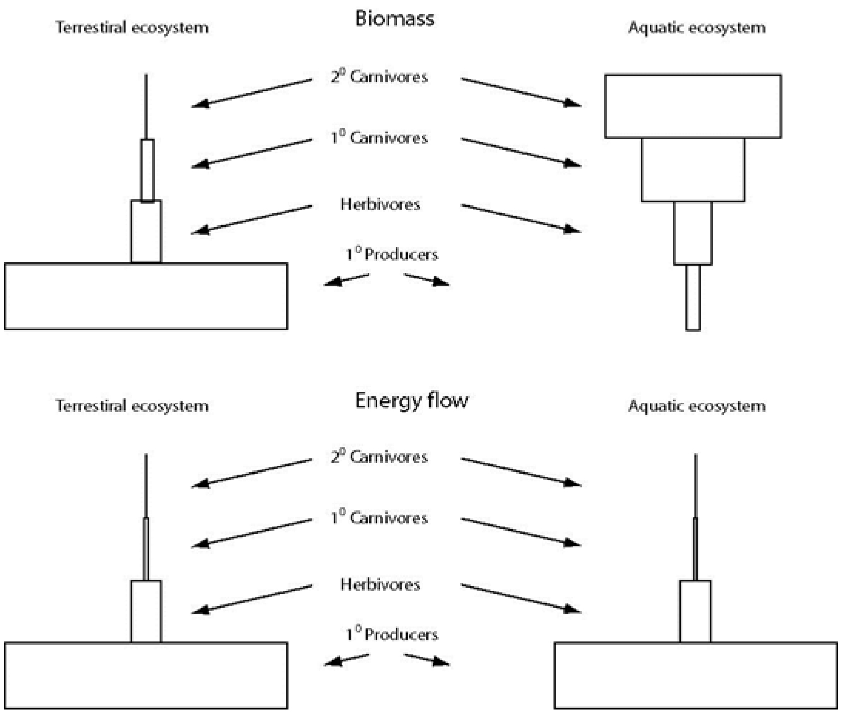


Figure 5.5: Energy pyramids are a result of inefficiencies in energy transfer through food chains. As predicted by the second law of thermodynamics, some energy is lost at every trophic level. (Source: Chapin et al; 2002)

Food chains can be classified in different ways. One way to look at them is on the basis of habitat type. In that sense we can talk about a food chain being aquatic or terrestrial. Aquatic and terrestrial food chains are illustrated and compared in Figure 5.6. Another way to look at food webs is based on whether they begin with grazing or with detritivory. Food chains that begin with grazing are referred to as grazing food chains while those that begin with detritivory are referred to as detrital or detritus food chains. These are detrital food chains and grazing food chains are compared in Figure 5.7.

The ultimate goal of studying food chains is to understand food web dynamics and how this relates with abiotic environment in ecosystem processes. Robert Paine (1980) has classified food webs into three major categories based on the focus that a researcher is interested in. These are Connectedness webs, Energy webs and Functional webs. These three types of webs are depicted in Figure 5.8. Connectedness webs are those in which all known links are drawn and equal importance is attached to each link for the purpose of the study being conducted. In contrast, energy webs are drawn with indication of which interactions are the strongest in terms of food consumed. One of the main pioneers the study of energy transfer in ecosystems is Raymond Lindeman. Lindeman pioneered the study of trophic dynamics i.e. the transfer of energy from one part of the ecosystem to another. Lindeman's pioneering paper "The Trophic -Dynamic Aspect of Ecology" published in 1942 is essential reading for every student of ecosystem ecology. Lindeman's work paved way for the study of energy transfer in ecosystems leading to the present day studies on energy transfer and efficiency that allow today's scientists to be able study the efficiency with which energy is transferred in ecosystems. In energy webs, strong links are indicated with thick lines.

High consumption is, however, not necessarily synonymous with importance. This is why Paine found it necessary to define a third category of food web: the functional web. Functional webs depict the importance of the links in a food web. By importance we are referring to how crucial a link is to the maintenance of the ecosystem in its existing state. Functional webs are different from both energy and connectedness links because some species are more important in food webs even though they are not the most abundant or most energy-yielding. These species are known as keystone species.

Another concept associated with food chains and food webs is the finding that some species within the web tend to have disproportionately more effect on the ecosystem than others. In other words, the removal of such species from an ecosystem will change the system much more profoundly than the removal of other species. Such species are referred to as Keystone species.

The functional food web is based on the keystone species concept. This concept is treated in more detail in Chapter 6.

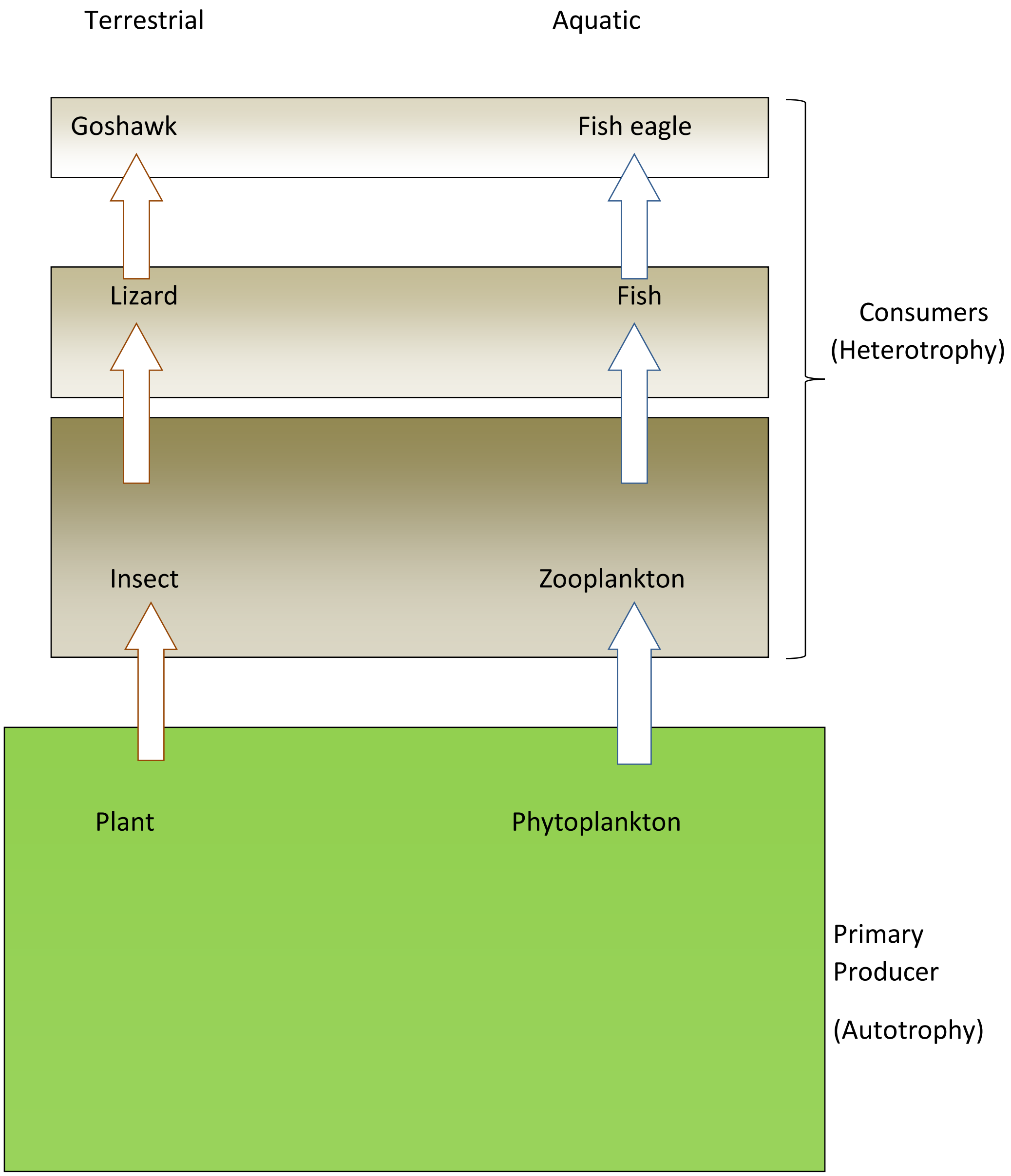


Figure 5.6: Terrestrial and Aquatic Food Chains compared

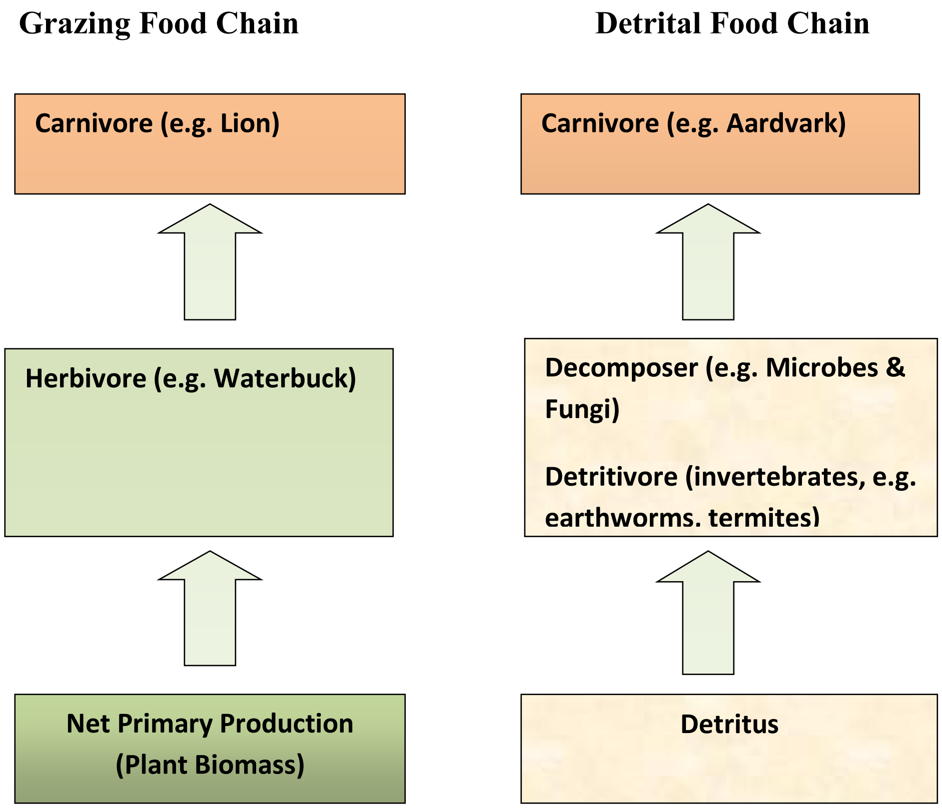
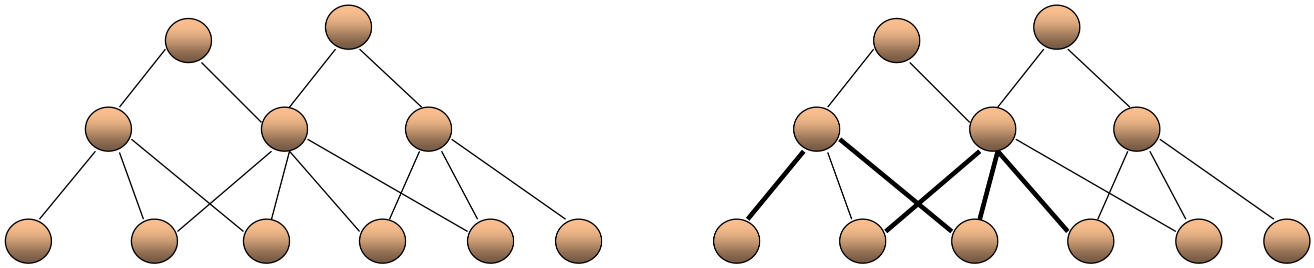
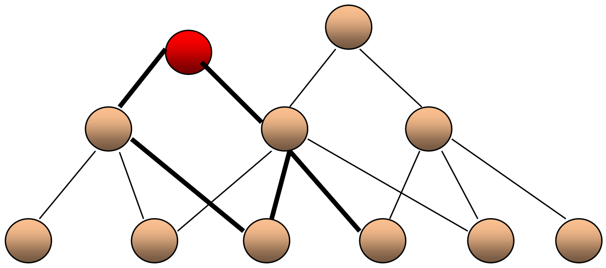


Figure 5.7: Detrital and Grazing Food Chains compared



(a) Connectedness web (b) Energy web



(c) Functional web ● = Keystone species

Figure 5.8: Connectedness, Energy and Functional Food Chains compared

5.3.NUTRIENT AND WATER CYCLING

Nutrients are the elements that are required for the reproduction, development and maintenance of organisms. Nutrients are continuously moving between and within ecosystems. During this process they are used, reused and transformed. The cycling of water in ecosystems is closely linked to that of other nutrients because most of them are water-soluble and are transported and absorbed as solutes in water. The two main processes are precipitation and evaporation. Both these processes are driven by solar radiation. Consequently water cycling is primarily a physical process whereas the cycling of most nutrients is primarily a chemical process. A second point to keep in mind is that water cycling is not only closely linked with nutrient cycling but also with energy transfer. Nutrient cycling is sometimes referred to as biogeochemical cycling. Figure 5.9 shows a generalized and simplified model of a biogeochemical cycling.

Cycling nutrients pass through biological, geological and atmospheric reservoirs. The biological reservoirs are the organisms within the ecosystem. This is the biotic component of ecosystems. Within the biotic component, nutrients move from one trophic level to another after primary biomass formation through the processes of consumption and decomposition. In the abiotic component the primary mechanisms for the release and movement of nutrients are weathering, burning and rock formation. In terrestrial ecosystems soil is the primary link between the abiotic and biotic components because through absorption and assimilation. In aquatic ecosystems assimilation is from dissolved nutrients in water and sediments.

5.3.1. The Biogenic Elements

In the last section we reviewed the general scheme of nutrient cycling. In this section we review the peculiarities in the cycling of four of the major elements that are essential for life. These elements are known as the biogenic elements because they are the most essential components of the biomass of living organisms. Biogenic elements are able to perform their essential functions because they meet definite criteria of atomic weight and reactivity. As a result, they are not randomly distributed in the periodic table of elements but form definite groups within the first five periods. This makes it possible to know whether an element is likely to be essential for life even before it is investigated. Some of the elements are required in small quantities and therefore are referred to as trace elements. Some are however required in relatively large quantities and are therefore referred to as major elements. The major elements are carbon, hydrogen, oxygen nitrogen phosphorus and sulfur (C, H, O, N, P, and S). The major elements are the most intensely cycled biogeochemically. The biogeochemical cycles of the major elements are not reviewed here in great detail. Instead we review briefly the key stages in each cycle and introduce some of the current areas of research interests in this subject

In addition to the major elements, we also briefly review the Water Cycle and how this is closely tied to the cycling of nutrients and the transfer of energy. Water is the solvent of life. All biogeochemical cycles have a stage in which water is involved. Furthermore, water itself, which is a compound of hydrogen and oxygen, is essential to the physiology of all living things. The cycling of water (the hydrological cycle) is therefore inextricably linked to nutrient cycling and energy transfer in ecological systems.

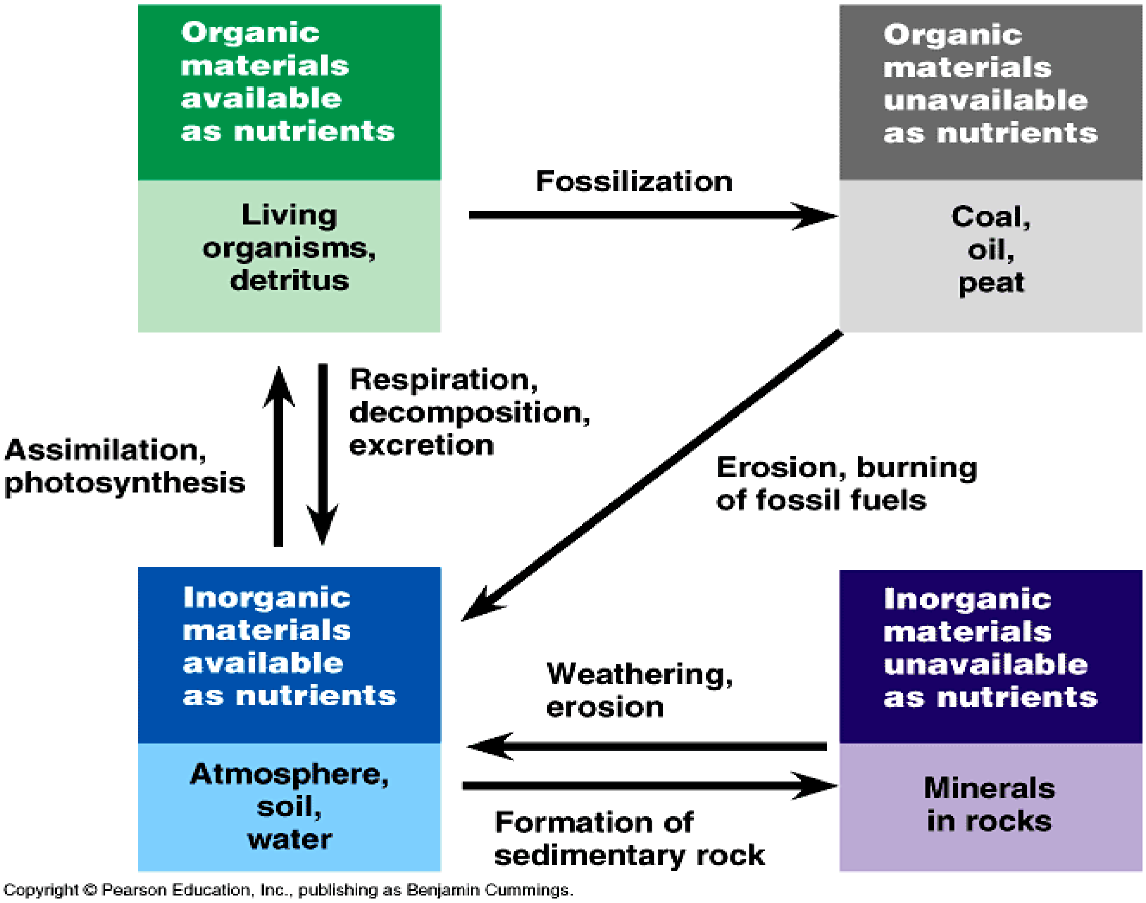


Figure 5.9: Generalized model of biogeochemical cycling. (Copyright: Pearson Education, Inc.)

The scheme presented in Figure 5.9 represents the pools and basic processes that are common to all nutrient cycles. Each of the nutrients, however, has some peculiarities in its cycling. These peculiarities are briefly reviewed in the next sections. In general, nutrient cycling occurs at local level through the action of biota and at the global level through geological and climatic processes such as atmospheric circulation, weathering and erosion. You may recall that these are the state factors that influence the interactive controls on ecosystem processes in Amundson and Jenny's state factor model.

5.3.2. Carbon, Hydrogen and Oxygen

The Carbon Cycle

Carbon cycles among biological, geological and atmospheric pools (Figure 5.10).The cycle is the continuous process by which carbon is exchanged between organisms and the environment. The circulation of carbon atoms in the biosphere is as a retsult of photosynthetic conversion of carbon dioxide into complex organic compounds by plants, which are consumed by other organisms. Carbon is then passed into the food chain and returned to the atmosphere by the respiration and decay of animals, plants, and other organisms. The burning of fossil fuels also releases carbon dioxide into the atmosphere. A key contemporary area of research that is related to the carbon cycle is in the role that elevated levels of atmospheric CO_2 is playing in ecosystems. Atmospheric CO_2 levels have continued to rise on Earth since (Figure 5.11)

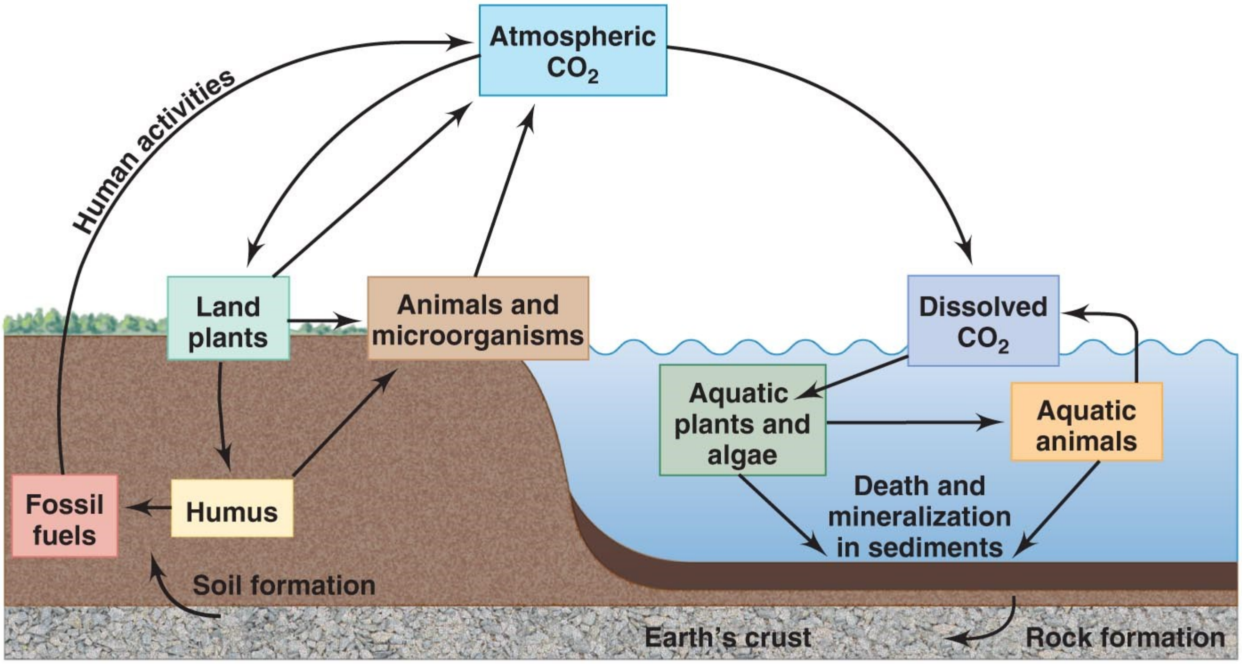


Figure 5.10: The Carbon Cycle (Source: Madigan *et. al*. 2009)

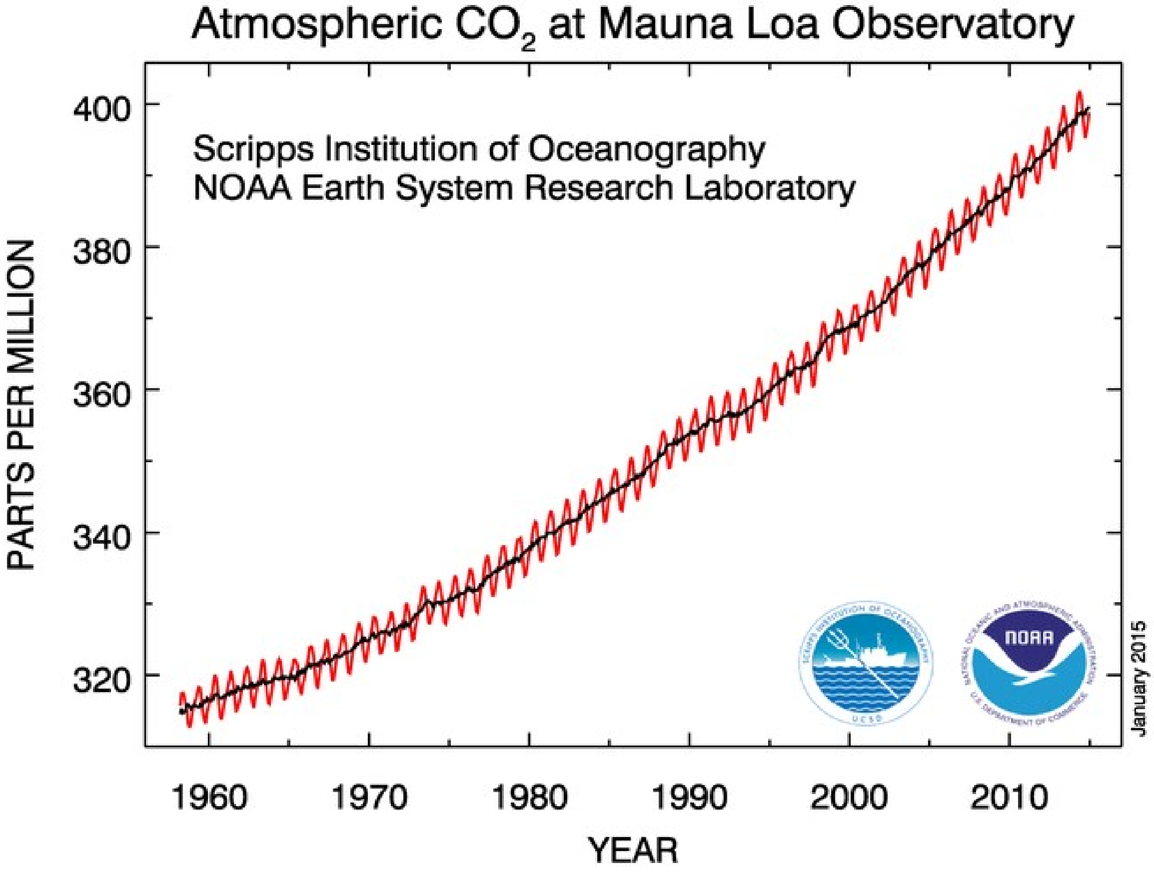


Figure 5.11: Atmospheric CO_2 1958-2014. Red = monthly average. Black =adjusted for seasonal changes. Source: Dr. Pieter Tans, OAA/ESRL (http://www.esrl.noaa.gov/gmd/ccgg/trends/) and Dr. Ralph Keeling, Schripps Institution of Oceanography (scrippsco2.ucsd.edu/).Via: http://www.c2es.org/science-impacts/basics

The Hydrogen Cycle

Globally, the largest reservoir of hydrogen is water. The most important processes for active cycling of hydrogen in water are photosynthesis and respiration. Cycling of hydrogen by these means is, however, very slow because of the large size of the reservoir involved. Water is present on the planet in very large reservoirs with the oceans being the largest of these. However, large amounts of water crystals tied up in rock lattices and polar ice are unavailable for cycling for long periods. Minor reservoirs of hydrogen include liquid and gaseous fossil fuels and organic matter, both living and dead. Biological hydrogen production is mainly as free gaseous H_2 produced in anaerobic fermentations and also as a side product of photosynthesis coupled with nitrogen fixation by cyanobacteria and by Rhizobium–legume mutualistic associations. The hydrogen gas produced anaerobically is mostly used to reduce NO_3^+, $SO_4^{2-,}$ Fe^{3+} and Mn^{4+} or to generate CH_4. In oxygenated soils or sediments, rising hydrogen gas is mostly metabolized oxidatively to H_2O therefore very little or none is able to escape to the atmosphere. Hydrogen is also produced anthropogenically when fossil fuels are burnt. Other ways in which hydrogen is produced include atmospheric photodecomposition of methane and the photodissociation of water vapor in the upper atmosphere. Hydrogen produced in the upper atmosphere is lost to outer space because the gravitational pull of the Earth is not strong enough to bring downward.

One interesting puzzle that could be of research interest is what happens to the double amount of hydrogen that is released when water is split to release oxygen into the atmosphere. 21% of atmospheric oxygen is known to be derived from the splitting of water during photosynthesis. Estimates of hydrogen in organic matter and fossil fuels reveal levels that are too low to account for the amounts released during photosynthetic splitting of water. Furthermore, no substantial hydrogen sinks have been found. One speculation is that the missing amount of hydrogen is most likely being lost to space.

The Oxygen Cycle

Like hydrogen, the origin of atmospheric oxygen is photosynthesis. Atmospheric oxygen is removed from the atmosphere by respiration. Respiration also produces CO_2. As a result the oxygen and carbon cycles are interconnected through the complementary activities of autotrophic organisms (producers) responsible for photosynthesis and heterotrophs (consumers) that use oxygen for respiration (Figure 5.12). Respiration not only produces CO_2 but also reconstitutes the water cleaved in photosynthesis. An interesting ecological question is why global elevated levels of CO_2 related to anthropogenic activities have not resulted in decreased availability of oxygen. The answer to this is that the atmospheric reservoir of oxygen (21% of the atmosphere) is very large compared to just 0.03% for CO_2. Estimates show that the burning of all global supply of fossil fuels will reduce oxygen levels by just 3% (Broeker, 1970).

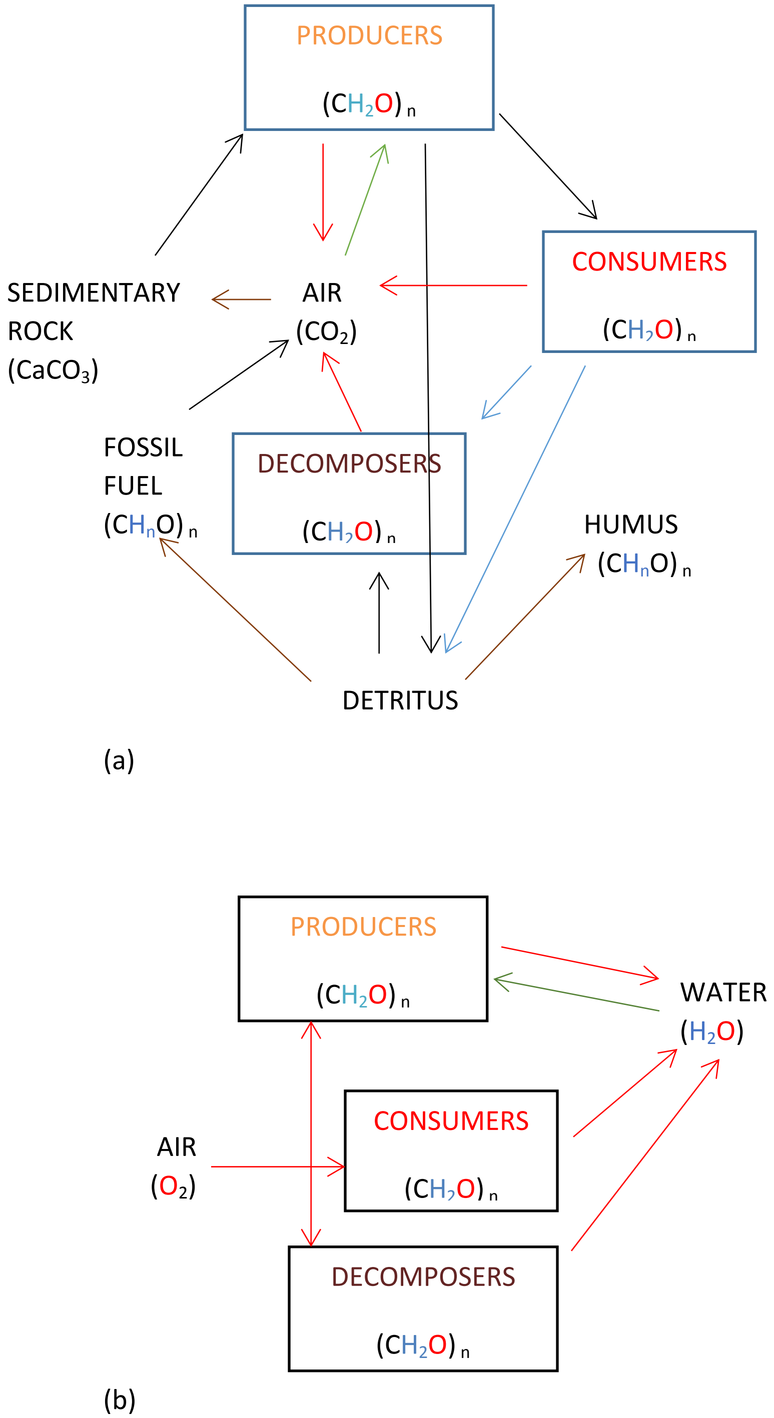


Figure 5.12: The Cycling of Oxygen, Hydrogen, Carbon dioxide and Water are closely linked. Carbon and oxygen come out of the air as carbon dioxide during photosynthesis and are returned during respiration. Oxygen is produced from water during photosynthesis and combines with the hydrogen to form water during respiration.

5.3.3. Nitrogen, Sulfur and Phosphorus

The Nitrogen Cycle

The nitrogen cycle is of particular interest to ecologists because its availability can affect the rate of key ecosystem processes, including primary production and decomposition. It is a part of all living cells and is necessary part of all proteins, enzymes and metabolic processes involved in the synthesis and transfer of energy. Nitrogen is a part of chlorophyll, the green pigment of plant that is responsible for photosynthesis and it helps plants with rapid growth, increasing seeds and fruits production and improving the quality of leaf and forage crops.

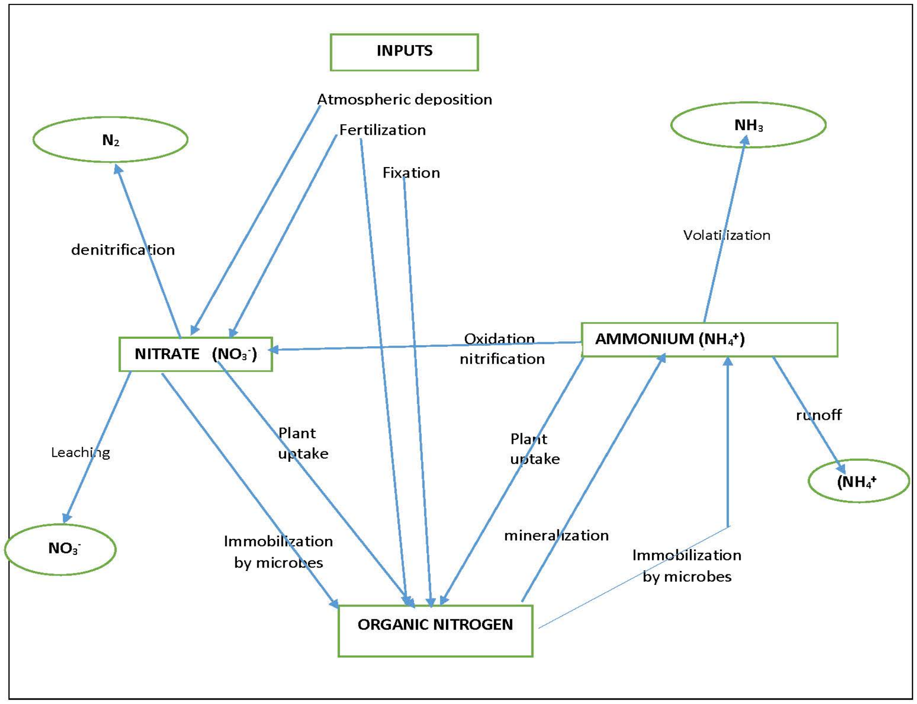


Figure 5.13: The Nitrogen Cycle

Nitrogen is present in the environment in a wide variety of chemical forms including organic nitrogen, ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), nitrous oxide (N_2O), nitric oxide (NO) or inorganic nitrogen gas (N_2). Organic nitrogen may be in the form of a living organism, humus or in the intermediate products of organic matter decomposition.

Nitrogen cycles (Figure 5.13) among biological, geological and atmospheric pools and its cycling is highly influenced by biological action of a relatively small number of species. These organisms are able to convert nitrogen into the form that is usable by other organisms in the ecosystem. These organisms (nitrogen-fixers) are very essential to ecosystem function because nitrogen gas (N_2) which makes up 78% of the Earth's atmosphere is not usable by organisms in that form. It must be broken down before its atoms can combine with other elements. This breakdown process is known as nitrogen-fixation. The ability to fix nitrogen is restricted to few species of bacteria, archaea, cyanobacteria and symbiotic associations such as those associated with leguminous plants. .

Nitrogen fixation

The conversion of atmospheric nitrogen (N_2) to the form in which it is readily available for plants' use is termed nitrogen fixation. This occurs through the industrial process (abiotic fixation) of the production of commercial fertilizers and biological process (Biological fixation). Biological fixation is said to occur in a process whereby series of soil microorganisms such as aerobic and anaerobic bacteria provide a direct source of ammonia to the plants. e.g. symbiotic bacteria such as *Rhizobium* that are found in the root nodules of legumes.

Decay and nitrification

Microbes decompose organic nitrogen, manure, organic matter and plant residues to ammonium. The process by which microorganisms convert ammonium to nitrate to obtain energy is called nitrification. Nitrate is the form in which nitrogen is mostly available to plants; however, it is also highly susceptible to leaching.

Assimilation

Nitrates are the form of nitrogen most commonly assimilated by plants through root hairs. This is taking up of nitrogen-based compounds and the usage of same to form tissues which are passed from one organism to another through consumption, as matter and energy transfers through the complex interconnected chains

Denitrification

Denitrification occurs when Nitrogen is lost through the conversion of nitrate to gaseous forms of nitrogen such as nitric acid, nitrous oxide and dinitrogen gas. Hence, denitrification corresponds to the part of the biological nitrogen cycle that is opposed to nitrogen fixation. The natural cycle of denitrification comprises a cascade of different enzymes that stepwise reduce nitrate to dinitrogen

Some potential areas of research relating to nitrogen include these potential harmful effects identified by the University Corporation for Atmospheric Research (NCAR, 2005):

- **Ecosystems**: Nitrogen additions to the soil can lead to changes that favor weeds over native plants, which in turn reduces species diversity and changes ecosystems. Research shows that nitrogen levels are linked with changes in grassland species, from mosses and lichens to grasses and flowers.
- **Precipitation**: Nitrogen oxides react with water to form nitric acid, which along with sulfur dioxide is a major component of acid rain. Acid rain can damage and kill aquatic life and vegetation, as well as corrode buildings, bridges, and other structures.
- **Air quality:** High concentrations of nitrogen oxides in the lower atmosphere are a precursor to tropospheric ozone which is known to damage living tissues, including human lungs, and decrease plant production.
- **Water quality:** Adding large amounts of nitrogen to rivers, lakes, and coastal systems results in eutrophication, a condition that occurs in aquatic ecosystems when excessive nutrient concentrations stimulate blooms of algae that deplete oxygen, killing fish and other organisms and ruining water quality.
- **Carbon cycle:** The impacts of nitrogen deposition on the global carbon cycle are uncertain, but it is likely that some ecosystems have been fertilized by additional nitrogen, which may boost their capture and storage of carbon. Sustained carbon sinks are unlikely, however, because soil acidification, ozone pollution, and other negative effects eventually compromise nitrogen-enhanced carbon uptake.

The Sulfur Cycle

The importance of sulfur as a macronutrient stems from the fact that it is an essential component of protein. Sulfur occurs in the atmosphere mainly as hydrogen sulfide (H_2S). Most H_2S in the atmosphere originates from volcanic eruptions and from deep sea hydrothermal vents. Decomposition is also an important source. H_2S in the atmosphere is readily oxidized to produce sulfur dioxide (SO_2). Since SO_2 is water soluble it dissolves in precipitation to become weak sulfuric acid. This is how sulfur returns to terrestrial and aquatic ecosystems from the atmosphere.

Another source of atmospheric sulfur is when SO_2 is emitted into the atmosphere from the burning of fossil fuels. In fact, this form of release by far outweighs that arising from the oxidation of H_2S in the atmosphere. Anthropogenic SO_2 emissions are so high in some regions that pH of precipitation has increased to much higher levels than normal. High acidity rain water arising from increased atmospheric SO_2 is referred to as 'Acid Rain' or Acid Precipitation. Acid precipitation can kill aquatic and terrestrial life and produce profound changes in ecosystem function. It is therefore a major area of research interest.

Another area of research interest on the sulfur cycle relates to the role the sulfurous gas dimethyl sulfide (CH_3SCH_3) usually referred to simply as DMS. DMS originates from dimethylsulfoniopropionate (DMSP) which is a major metabolite of marine algae. Researchers are interested in the potential for using DMS to reduce global warming caused by greenhouse gases such as CO_2. This potential lies in the fact that particles of DMS in the atmosphere form nuclei around which water vapor condensation occurs leading to the formation of clouds. Since DMS is produced by the action of marine algae that can occur in vast numbers, many scientists believe that the potential exist to use this approach to greatly increase cloud cover as a way of countering global warming.

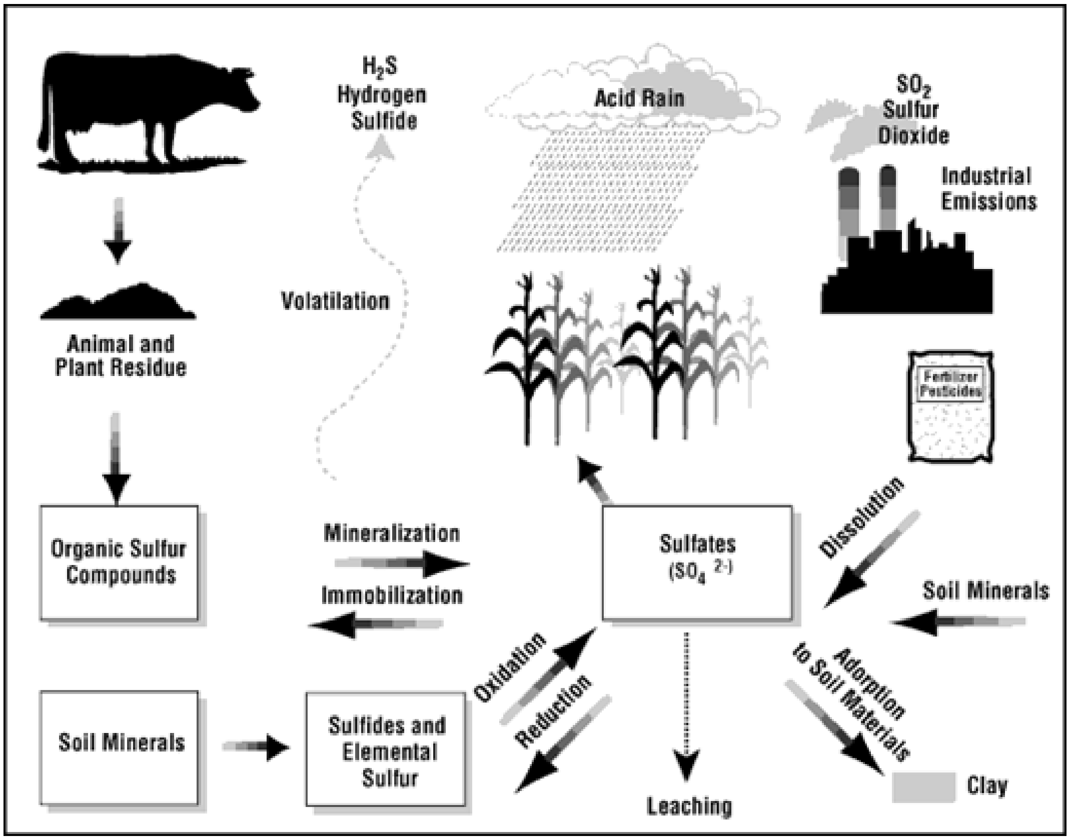


Figure 5.14: The Sulfur Cycle

Image obtained from http://www.agnr.umd.edu/users/agron/nutrient/Factshee/sulfur/Sulfur.html

The Phosphorus Cycle

Phosphorus is a very important element for life because it is incorporated in key biomolecules ATP, DNA, RNA and the phospholipid bilayer of cell membranes. It cycles locally between geological and biological components of ecosystems. Its cycle has no atmospheric component since there is no gaseous phase in it. The largest pool of phosphorus is the Earth's crust. It is released into the soil from this pool through weathering and erosion. Plants absorb phosphorus from the soil. Herbivores get their requirement from consuming plants. The herbivores are consumed by carnivores. Decomposition of detritus returns the phosphorus into the soil where it becomes available for absorption by plants. Phosphorus is washed into aquatic ecosystems through leaching and runoff

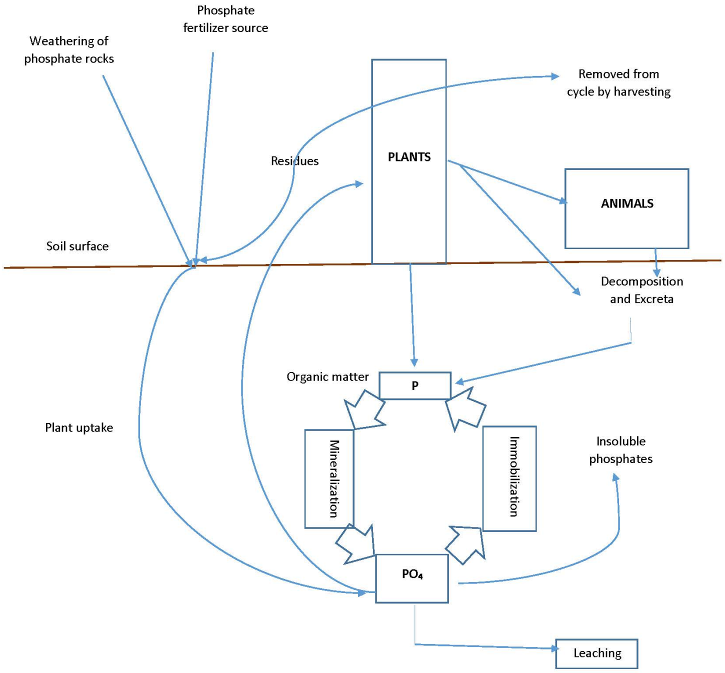


Figure 5.15: The Phosphorus cycle

Phosphorus and Nitrogen are two of the most limiting macronutrients in both aquatic and terrestrial ecosystems. A major reason why phosphorus is limiting in nature is that its availability is restricted by its tendency to precipitate in the presence of bivalent metals such as Ca^{2+} and Mg^{2+} and ferric (Fe^{3+}) ions at neutral to alkaline pH.

An interesting hypothesis associated with nutrient availability in general and nitrogen and phosphorus in particular (because of their limiting nature) is the Nutrient Hot Spot Hypothesis. According to this hypothesis certain habitats within ecosystems are nutrient or biogeochemical cycling hotspots. Such habitats are therefore of greater significance in to ecosystem functioning. Examples of nutrient hotspots include roosting and nesting habitats of birds where guano piles up and beaver ponds because of their high organic matter retention times. The concept of Nutrient hotspots is therefore closely related to that of keystone species.

5.3.4. The Hydrological Cycle

Water is a compound made of hydrogen and oxygen. We have already discussed the cycling of these two elements. Since the cycling of oxygen is closely linked to that of CO_2, it becomes obvious that the cycling of water, oxygen, hydrogen and CO_2 are intricately linked in nature. Nevertheless, the water cycle also known as the hydrological cycle is largely a physical process of evaporation and precipitation. This process is fueled by the sun's energy.

The hydrological cycle has a huge influence on biogeochemical cycling because many of the biogenic macronutrients or compounds involved in their cycling are soluble in water. Also, water is a limiting factor in the abundance and distribution of many organisms on the planet. This issue was reviewed when we discussed the role of climate as state factor.

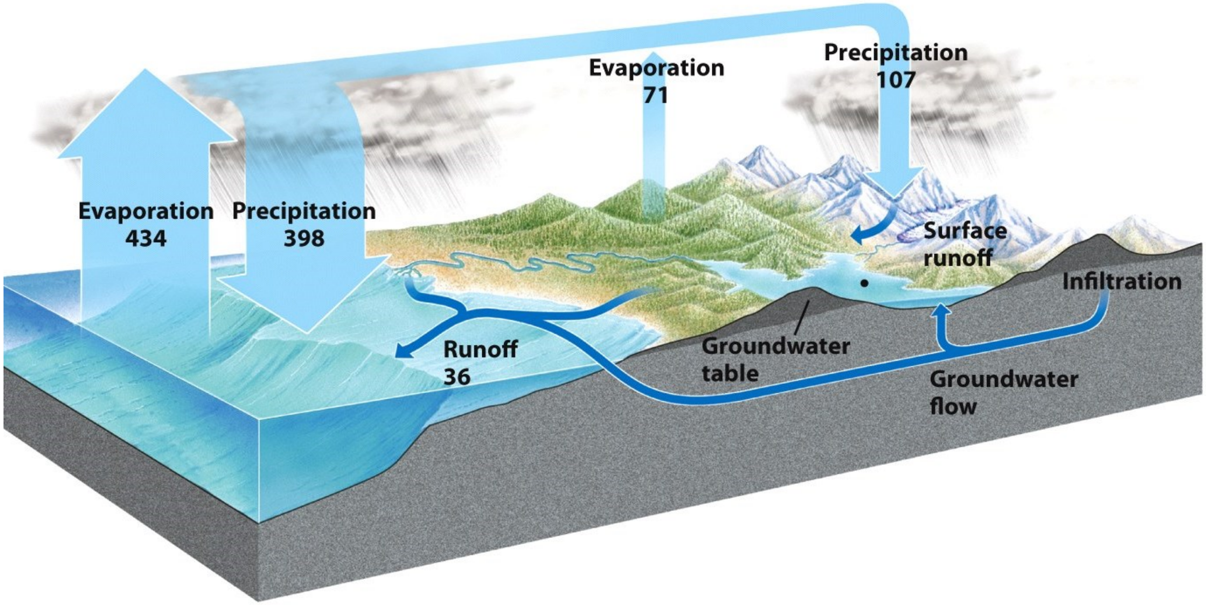


Figure 5.16: Global Hydrological Cycle (Copyright 2010 W. H. Freeman and Company)

Chapter 6: Controls on Ecosystem Processes

6.1. A FRAMEWORK FOR ANALYSIS

A useful framework for the analysis of the factors that control ecosystem processes is that developed by Jenny (1941), Amundson and Jenny, 1997) and elaborated by Chapin *et al* (2002). The framework identifies at least five independent control variables that influence ecosystem processes. They call these variables state factors. According to Amundson and Jenny (1997) climate, parent material (from which soil is formed), topography and potential biota (the species that have the potential to occupy an ecosystem) and time are state factors that determine the characteristics of an ecosystem.

State factors influence ecosystem functioning through their effects on interactive controls on ecosystem processes. This relationship is depicted in Figure 6.1.

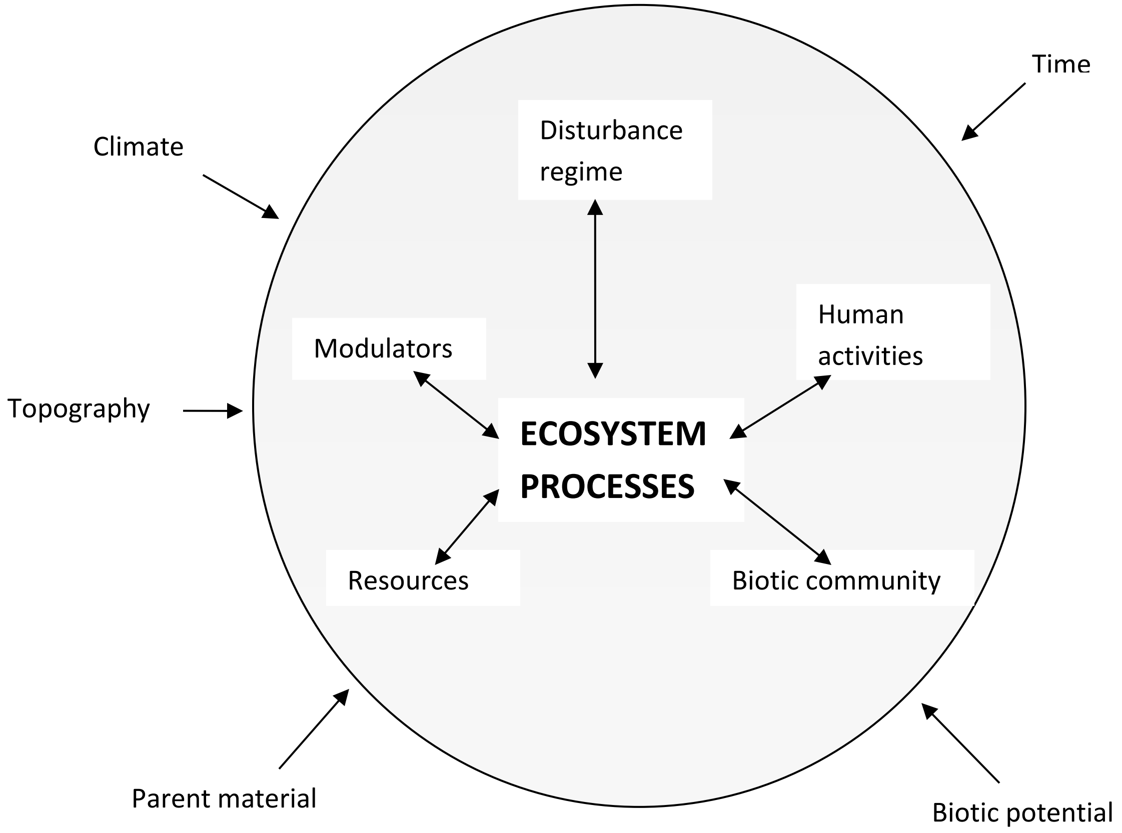


Figure 6.1: Ecosystem state factors (outer circle) and their relationship with interactive controls (inner circle) on ecosystem processes. (Adapted from Chapin *et al*, 2002; based on Jenny (1941) and Amundson and Jenny (1997)

Interactive processes which are shown in the inner circle are modulators, disturbance regime, human activities, resources and biotic community. In this chapter we examine how these controls interact to control the key processes that drive energy flow and nutrient cycling in ecosystems. These are the processes that link the biotic and abiotic pools within ecosystems. They are primary production, consumption, decomposition and assimilation.

Resources are the energy and materials in the ecosystem. Organisms use materials (nutrients) and energy for growth and maintenance. In chapter 5 we saw how materials are cycled and energy is transferred. The amount of energy and materials within an ecosystem and how they move from one pool to another are all influenced by state factors through their effects on interactive controls and by the interactions of the controls themselves.

The disturbance experienced by an ecosystem is another control factor that interacts with other controls to affect ecosystem processes. Ecosystem disturbance includes events such as fire outbreaks, pest outbreaks, floods, species removals or introductions and many other natural and man-made phenomena. Modern human activities, which are one of the interactive controls, are actually a special form of disturbance. They get the status of a category as a result of their sheer magnitude, pervasiveness and increasing significance as controls on ecosystems in today's earth. Disturbance is usually followed by ecological succession.

Modulators are the physical conditions that influence the magnitude and significance of other controls. Examples of modulators include factors such as temperature, humidity, salinity, acidity, soil texture etc. They are the conditions existing within habitats. The conditions themselves arise as a result of the combined effects of the state factors.

Biotic community is the species existing within the ecosystem. The biotic community is derived from the biotic potential (a state factor) and comprises species that were able to disperse and establish themselves in the ecosystem. The biotic community influences and is influenced the other interactive controls. From the ecological perspective, the bottom line in the understanding of controls affecting ecosystem processes is how this translate into effects oh biotic characteristics such as species diversity and the sustenance of the ecosystem processes that are essential to the sustenance of life on earth. In the rest of this chapter we present examples of how interactive controls work together to control the essential ecosystem processes that drive the flow of materials and energy through ecosystems and thereby sustain life on earth i.e. primary production, consumption, decomposition and absorption.

Ecosystems are complex systems primarily because controls on the processes that operate within them are so interactive. Controls on ecosystem processes can only be understood within the context of how they interact to produce observed outcomes. For example, at the global level, climate determines the distribution of biomes while geology determines the nature of parental material. At local levels soils (which is a legacy of parent material), vegetation cover (which is highly influenced by climate) and topography and the legacy of human activities combine to create microclimatic conditions that determine moisture availability, ambient temperatures and other conditions within specific habitats. These microclimatic conditions in turn determine the types of species that are able to colonize and persist in such habitats.

Interactive controls therefore create chains of effects connected through feedbacks within the system. Effects initiated by one control in turn trigger changes in another leading to a cascade of change within the system. Feedback mechanisms enable the system to self-organize tending towards stability. One way to look at the influence of interactive controls is to look at the implications of changes within the ecosystem on each of them. in the rest of this chapter we examine how biotic and abiotic changes within the ecosystem affect each resource supply, modulators and the biotic community. We also examine the role of disturbance on the ecosystem

6.2. EFFECTS ON RESOURCE SUPPLY

The amount of energy and materials in the biotic and abiotic pools within an ecosystem are determined first of all by primary production and then by the processes that drive energy transfer and nutrient cycling within the system namely consumption, decomposition and absorption. Each one of these processes is influenced by other control factors. These factors combine to determine the amount of resources that are available within the ecosystem

6.2.1. Controls on Primary Production

Net primary production in terrestrial ecosystems is limited mainly by precipitation (Figure 6.2), temperature (Figure 6.3) and nutrient availability. In aquatic ecosystems the main limitations are light and nutrient availability (Figure 6.4). Light is an important factor in aquatic environments because of the capacity of water to absorb it making less available with increasing depth (Figure 6.5). Despite the significance of light, however, nutrient availability appears to be a more significant factor in aquatic environments. This evident from the fact that oceanic chlorophyll concentrations are low in tropical waters despite the high regimes of light in these locations. Nitrogen and Phosphorus appear to be the most important nutrients limiting both aquatic and terrestrial primary production. In marine environments iron is also an important limiting factor (Downing, 1999). The relations between these limiting factors and primary production are presented in Figures 6.2 to 6.4.

Atmospheric carbon dioxide levels have also been linked to increases in primary productivity. The effect of increased CO_2 tends to be interactive with other factors. For example, data from Smith et al (2000) show that increase in growth of the Creosote bush *Larrea tridnentate* in elevated CO_2 experimental plots coincided with years of high rainfall. The researchers used Free-Air CO_2 Enrichment (FACE) technology to conduct experiments in which CO_2 levels were artificially elevated in experimental patches of a forest.

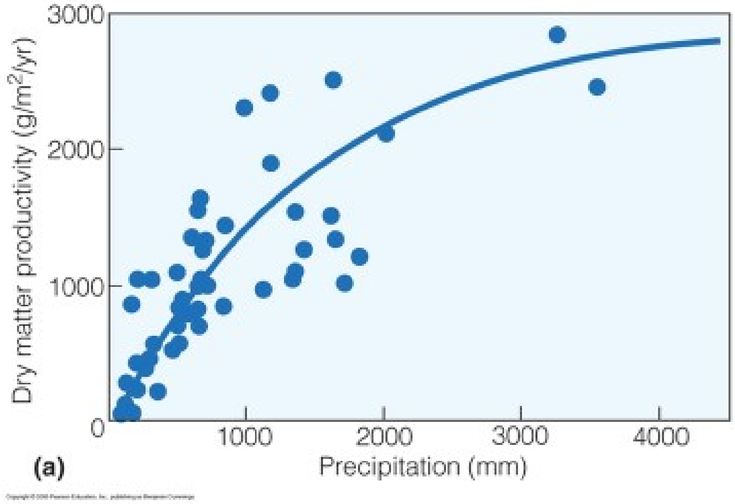


Figure 6.2: The relationship between primary productivity and precipitation (Source: Campbell and Reece, 2003)

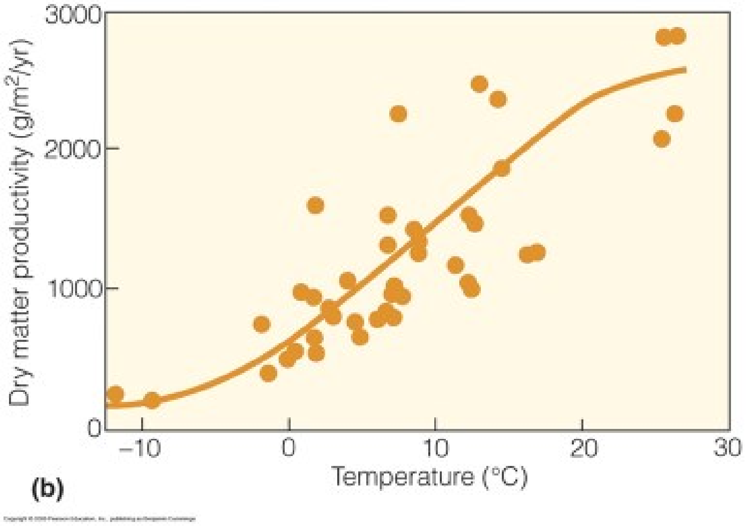


Figure 6.3: The relationship between primary productivity and Temperature (Campbell and Reece, 2003)

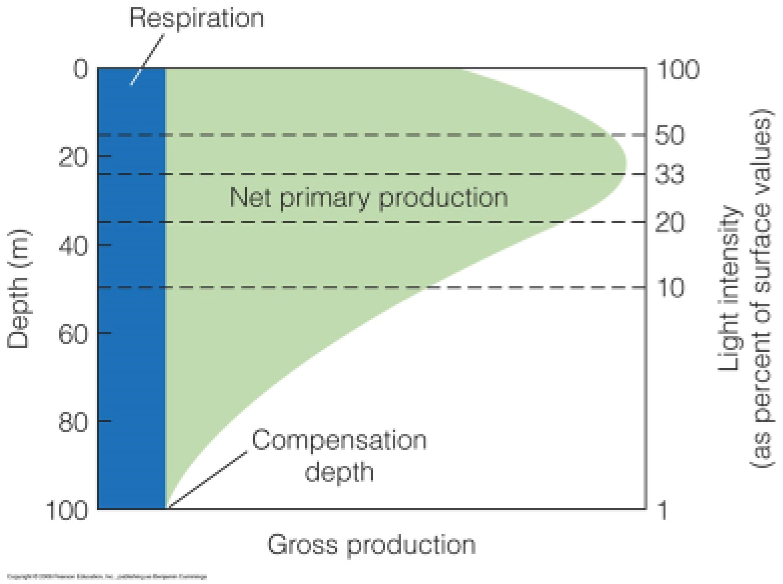


Figure 6.4: Controls on primary production in aquatic environment. Decline in light intensity with increasing depth constitutes a limitation to gross production at different depths. (Campbell and Reece, 2003)

6.2.2. Controls on Decomposition and Nutrient turnover

Decomposition is the physical and chemical breakdown of dead plant, animal and microbial matter (known as detritus). Two distinct mechanisms are involved in the breakdown of detritus. The first is the physical fragmentation of detritus by detritivores. Detritivores are mostly invertebrates such as termites, ants, earthworms and beetles. The second mechanism is the microbial decomposition detritus fragments by bacteria and fungi. Fragmentation of detritus increases its vulnerability to microbial action by creating fresh surfaces for microbial colonization increasing the proportion of litter mass that is accessible to microbial action. Fragmentation also creates routes for entrance for microbe since non-fragmented leaves for example are covered with lignin which is recalcitrant to microbial attack.

Decomposition rates are influenced by leaf litter temperature, moisture content, microbial diversity, detritivore availability, plant species, and many other control factors. These factors work together to determine spatial and temporal variations in the rates of decomposition in ecosystems. Rising temperatures for example can lead to exponential increase in populations of microbes responsible for litter decomposition if moisture replenishment rates are high enough to prevent drying of litter. Controls on moisture availability therefore combine with rising temperatures to either accelerate decomposition rates or lead to drying of litter and the slow down or halting of the process. Moisture status of the decomposition site is influenced by soil characteristics and both moisture content and temperature are affected by vegetation cover.

Disturbance can also interact with soil moisture and temperature and through this means affect the rate of decomposition. For example, physical shifting of soil by invertebrates such as earthworms may increase deposition rates by promoting soil aeration and by exposing new surfaces to microbial activity.

Availability of resources may also play a key control role in decomposition. One way in which this could happen is through variation in leaf litter quality. Plant species vary in the content of recalcitrant compounds such as lignin in their leaves. This variation plays a key role in determining rates of decomposition of leaf litter. Species with high allocation of resources to leaves and those in which leaf life-span is short tend to have high concentrations labile compounds and low concentrations of recalcitrant cell compounds such as lignin (Reich *et al*, 1997). Litter from species which are adapted to low soil nutrient conditions decomposes slowly because of the negative effects on microbial populations within such soils. Low concentrations of nitrogen and phosphorus and high levels of lignin, tannin, waxes and other recalcitrant or toxic compounds all slow done the growth of the populations of the microorganisms needed for litter decomposition.

6.2.3. Controls on Uptake of Nutrients

Autotrophs absorb nutrients from the surrounding environment and convert them into biomass using energy from solar radiation. In terrestrial ecosystems, these nutrients, which mostly are the end products of decomposition and weathering, are absorbed by plants via their root systems in soil.

Several control factors work together to determine the quantities of nutrients present in soil and their absorption by plant root systems. Biotic determinants of soil nutrient content and its uptake by plants include resource-based mutualisms plant-mycorrhizae and plant-nitrogen-fixing bacteria relationships enhance the supply of nutrients and water to the plant. Allen and Allen (1986) studied the way mycorrhizae affect water extraction by the grass species *Agropyroon smithii* in the presence or absence of mycorrhizae. The result shows that, in the presence of mycorrhizae, the plant maintained higher leaf potential than in its absence. This finding appears to suggest that under similar soil moisture conditions, the presence of mycorrhizae enhanced water uptake ability of plants. A possible explanation for this is that mycorrhizae enhanced root access to phosphorus. Plants that have greater access to phosphorus tend to develop more extensive and finer roots that make them more efficient in extracting water from soil.

While mycorrhizae enhance water and nutrient supply to plants, the mutualism between plants and nitrogen-fixing bacteria enhances the supply of a specific nutrient; nitrogen.

6.3. EFFECTS FROM BIOTIC COMMUNITY CHANGES

6.3.1. Models of Control of Community Organization

One of the key questions relating to biotic community control on ecosystem processes is how biotic organization is controlled. There are two major hypotheses on how this happens. The first one postulates that community structure is controlled by what happens to the bottom trophic level. This model is known as the bottom-up model. The other hypothesis postulates that control of community structure is from the top trophic level and happens in a unidirectional way down to the bottom trophic level. This is known as the top-down model. To explain these two opposing views let us look at some hypothetical situations.

Consider the following hypothetical relationships between herbivores and the vegetation they consume:

(i) Situation 1: let us represent this situation by the expression V → H. In V → H increase in biomass vegetation leads to increase in the number or biomass of herbivores but not vice versa. These means that herbivore number or biomass is limited by vegetation but does not limit vegetation biomass.

(ii) Situation 2: let us represent this situation by the expression V ← H. In V ← H increase herbivore numbers or biomass leads to a decrease in the abundance of vegetation but not vice versa

(iii) Situation 3: let us represent this by the expression V ↔ H. In V ↔ H, feedback is in both directions i.e. vegetation biomass is sensitive to herbivore consumption and herbivore numbers or biomass are sensitive to changes in vegetation biomass

According to the bottom-up model, control is from the V → H linkage. This model postulates a unidirectional influence starting with the bottom trophic level and moving upwards. For example, in a food chain that begins with nutrients in soil and ends with a large predator such as a lion, the population of lions in a specified community will ultimately depend on soil nutrient levels. According to this view, all things being equal, the addition of fertilizer to soil should culminate into a reciprocal rise in predator numbers or biomass.

Using our expressions from above, the simplified bottom-up model is expressed as:

$N \rightarrow V \rightarrow H \rightarrow P$

Where: N is the nutrients

V is vegetation

H is herbivores

P is predators

In the bottom-up model the effect of addition or removal of predators does not extend all the way down to the bottom trophic levels. This means that in bottom-up controlled communities, it is only changes to the lower trophic levels that affect community structure.

The top-down model argues differently. According to this model, it is changes to the top trophic levels that alter community structure. According to this model predation is the main control on community structure because it limits the number of biomass and allows increases in vegetation biomass leading to increased depreciation of soil nutrient levels. The simplified top-down is expressed as:

N ←V← H← P

The top-down model of the control of community organization is also referred to as the trophic cascade hypothesis. Trophic cascade hypothesis predicts that the removal of a predator will produce a cascade of responses starting from top to the bottom trophic levels. This cascading effect is illustrated in Figure 6.5.

Trophic cascading has been used successfully in biomanipulation programs for the improving water quality

The outcome of community organization, regardless of whether control is top-down or bottom-up is leads it re-shapes community characteristics. It is these changes in characteristics of the biotic community that translate into implications on ecosystem processes. Changes in community structure and function are primarily driven by changes in species diversity. Many aspects of diversity such as species richness, species composition, species traits, and functional groups within a biotic community have been shown to directly or indirectly affect ecosystem processes. As a result, ecologists have spent a great deal of time trying to understand the factors that control species diversity in communities. Many hypotheses have been put forward. These include: the diversity-stability hypothesis, the keystone species hypothesis, the rivet hypothesis, and the redundancy hypothesis. Others are the Janzen-Connell hypothesis, the species-time hypothesis, the species-area hypothesis, the species-energy hypothesis,

Some of these hypotheses attempt to explain how species diversity is achieved while others try to explain how it is structured and the implications of alterations to its structure. Others such as the diversity-stability hypothesis attempt to do both. For example, the Janzen-Connell hypothesis, the species-time hypothesis, the species-area hypothesis and the species-energy hypothesis all attempt to explain why species diversity is higher in some ecosystems than in others. The rivet hypothesis, the keystone species hypothesis and the redundancy hypothesis, on the other hand, attempt primarily to predict the likely consequences of alteration of the species diversity of an ecosystem. Nevertheless, the question of why diversity is higher in some places than in others and the implications of diversity alteration are closely related. There is, therefore, a great deal of overlap between the two categories of hypotheses. In the next sub-section we examine the role that species diversity plays in the control of ecosystem processes and review some of the hypotheses that have been put forward in relation to this aspect.

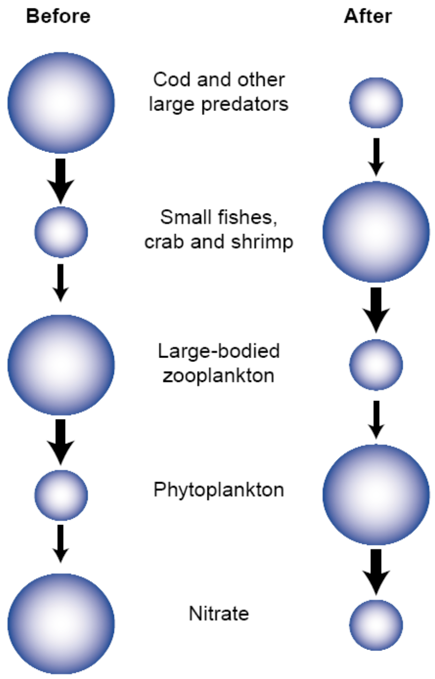


Figure 6.5: The trophic cascading in an aquatic ecosystem. Reduction in top predator population led to reduction in nitrate levels (Source: Schefer *et al*, 2005)

6.3.2. Controls via Species Diversity

The relationship between species diversity and ecosystem processes is one of the widely studied areas of ecology. Species diversity is linked to ecosystem processes through its effect on community structure and functioning. Higher diversity is said to enhance ecosystem stability. Charles Elton (1958) was the first to put forward this argument. He proposed the diversity-stability hypothesis. According to this hypothesis, the more species a community contains the more stable it is. Stability is defined as the ability of an ecosystem to maintain a steady state despite disturbance. Stability may result from resistance to disturbance or from resilience to disturbance. Resistance is the ability of a community or ecosystem to maintain its structure and functioning under pressure from potential disturbance. An ecosystem or community is also regarded as being in a stable if it is able to return to reorganize and resume function after an episode or several episodes of disturbance. Disturbance is any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment (White and Pickett, 1985). The diversity-stability hypothesis argument, therefore, is that ecosystems with greater diversity of species will be more resistant or resilient to disturbance.

The diversity-stability hypothesis raises two key questions. Does higher species diversity really enhance community and ecosystem stability? And how is species diversity controlled in communities and ecosystems? These two questions are dealt with in the rest of this section.

One of the most recent studies of the relationship between species diversity and community function was conducted by Shahid Naeem at Imperial College at Silwood Park outside London in the United Kingdom. Naeem *et. al*. (1994) conducted experiments in a specially designed facility called an Ecotron. The Ecotron contained 14 chambers in which environmental conditions were controlled. Conditions in all the chambers were kept exactly the same except for species richness in each of them. Figure 6.4 shows the design of the experiment. Three levels of species richness; high, medium and low were used.

Each treatment or model community had 4 trophic levels namely predator/parasite, herbivores, plants and decomposers. They used organisms that are most realistic for the chamber dimensions in the experiment such insects, snails and slugs as herbivores, parasitoids as predators and earthworms as decomposers and ran the experiment for 6 months. Species were added to the chambers as their feeding level became established. For example, predators were only added after the herbivore populations became established and herbivores were only added after plants had established.

Parameters measured included plant growth, community respiration, decomposition nutrient retention and other ecosystem processes. One of the key findings of the Ecotron experiment is that species rich communities were more productive than species poor communities.

The results obtained by Shahid Naeem and his colleagues were very interesting but needed to be confirmed from field studies. In 1996 David Tilman and his colleagues (Tilman *et al*, 1996) carried out field experiments in which they studied the relationship between species richness and community function. They sowed seeds of prairie plants in 3 x 3M plots on the same type of soil. The plots were sowed with various numbers of species. The lowest species composition was 1 while the highest was 24 species. The used percent cover as the measure of productivity of the various plots. Percent cover is the percent of ground that is covered by plant biomass. Their study showed that plots with higher species richness had higher percent cover than those with lower richness.

One of the explanations proposed for increased productivity that accompanies increased species diversity is species complementarity. The species complementarity argument is that increasing species also leads to increasing diversity in morphological, physiological and life-history forms. The result of this is that species complement each other to achieve much higher levels of nutrient extraction leading to higher combined nutrient use levels in species rich communities than in species poor ones.

Species complementarity is not the only proffered explanation for increased productivity accompanying higher species richness. An alternative explanation is known as the sampling effect. According to this opinion, species-rich communities are more likely to contain high performing species or “superspecies”.

Many studies of the relationship between species diversity and ecosystem function have since been carried out since the early studies previously described were conducted in the 1990s. Most studies confirm that increased species richness is positively correlated with higher productivity up to a certain limit. Nevertheless, the mechanism through which this effect happens is still a matter of debate. Further work needs to be done to determine what roles sampling effect and species complementarity play in this context.

Given the significance of species diversity to ecosystem functioning, a logical next line of investigation is what controls species diversity. Several patterns have been observed in nature and these have led to many hypotheses. One of the most universally observed patterns is the relationship between environmental complexity or spatial heterogeneity and species diversity. Spatial heterogeneity, and the habitat diversity associated with it, has been shown to correlate positively with species diversity. One of the first ecologists to observe this relationship was Robert H. MacArthur. MacArthur carried out many studies from a wide range of geographical areas. He measured diversity using the Shannon-Wiener index and foliage height diversity as his measure of environmental complexity (spatial heterogeneity). MacArthur and his colleagues studied this relationship in many locations in North America, Central America and in Australia.

In one of his studies, carried out in Florida in the USA and also in Panama in Central America MacArthur and his colleague (MacArthur and MacArthur, 1961) compared bird species diversity to foliage height in vegetative communities ranging from grassland to mature deciduous forests. Their study showed that bird species diversity was higher in study sites with greater diversity in foliage height. This was also the pattern found into other studies including the ones that were conducted in Australia. Since MacArthur’s work, many studies have been conducted in a wide range of biomes across the world with similar results. However, this phenomenon has only so far been demonstrated with animal species. Does environmental complexity enhance microbial and plant diversity? Intuitively the answer to that question has to be yes. The effect of spatial heterogeneity which characterizes environmental complexity appears to be that it facilitates niche partitioning thereby reducing competitive exclusion.

As we know, not everything that is intuitive is correct. One of the real paradoxes of nature that appears to contradict the above line of reasoning is the case of phytoplankton. G.E. Hutchinson in one of his publications (Hutchinson, 1961) refers to it as the “paradox of the plankton”.

Phytoplankton, which are primary producers, occupy habitats that are virtually devoid of spatial heterogeneity. Their habitats are open waters of lakes and oceans with little or no zonation. They all compete for the same nutrients and yet their species diversity is staggering. How do they manage to coexist without competitive exclusion? The phytoplankton paradox also applies to other primary producers. The plant species diversity of the tropical rainforest is a case in question. What controls plant species diversity in the tropical rainforest. Several hypotheses have been put forward. The most prominent one is the Janzen-Connell hypothesis. The Janzen-Connell hypothesis was initially proposed to explain the high species diversity that exists in tropical forests. However, many studies have since been conducted to test its predictions in other ecosystems. Other hypotheses exist that try to explain how species diversity is controlled in general and not specifically for tropical forests. These include the keystone species hypothesis and the diversity-stability hypothesis (which we examined at the beginning of this section). Others are the rivet hypothesis, the redundancy hypothesis, the idiosyncratic hypothesis, species-area hypothesis, the species-time hypothesis and the species-energy hypothesis

The Rivet Hypothesis

The rivet hypothesis was first proposed by Ehrlich and Ehrlich (1981). This hypothesis postulates that species in a community are like the rivets on the wing of an airplane. First of all some rivets are more crucial than others. In other words there are some rivets whose removal brings the aircraft wing closer to total disintegration than others. Secondly all rivets contribute to strengthening the aircraft wing and therefore the loss of anyone of them actually weakens the aircraft wing to some extent. Finally the more rivets removed the weaker the aircraft wing gets until a point is reached when the wing completely disintegrates. The rivet hypothesis does not explain how diversity comes about but argues for the avoidance of species loss since the point at which this loss will get before total ecosystem disintegration ensues cannot be predicted.

The Redundancy Hypothesis

The redundancy hypothesis postulates that in any community there are likely to several species that play the same functional roles. Therefore, the loss of a species can be compensated by another species with similar functional role as the extinct one. The species lost are said to be redundant because their loss is compensated by another species taking their place thereby preventing any significant changes in ecosystem functioning.

The Idiosyncratic Hypothesis

The idiosyncratic hypothesis argues that community services change as the number of species diversity increases or decreases but that the direction of such change cannot be predicted.

The Keystone Species Hypothesis

One of the really significant discoveries in ecology is that in many biotic communities a few species tend to exert disproportionately more pressure on community structure than the rest of the other species. These species are referred to as keystone species. Word keystone is borrowed

from the language of builders and refers to the stones in a building that must absolutely be in place in order that other stones stay where they are placed. Like keystones in a building keystone species in a community are usually few but have a disproportionate impact on the community structure. American ecologist Robert Paine (1966, 1969) was the first to propose the keystone species hypothesis. He proposed that the feeding activities of a few species have inordinate impact on community structure. Paine called these species keystone species. His argument was that predators may keep prey populations below their carrying capacities thereby preventing competitive exclusion from taking place. This he argues will in turn enable more species to coexist than would otherwise be the case. It is therefore expected that communities with high numbers of predators will have greater species diversity than those without.
Paine tested his hypothesis in two stages. First, he examined the relationship between species diversity and the relative proportion of predator numbers or activity in communities. Secondly, he conducted experiments in which he removed predators from some communities then compared species diversity from those and similar communities in which predators had not been removed. In his correlational studies, Paine found that in many cases communities in which predation was high tended to have higher diversity of species than those in which predation was low. For example, he observed that the zooplankton community in the Atlantic Ocean continental shelves included 81 species 16% of which were predators. In contrast, the Sargasso Sea which had 39% predator species contained 268 species in total. Correlation of course is not causation. To properly test his hypothesis, Paine needed to conduct experiments. Paine conducted one of his experiments in a place called Mukkaw Bay in Washington, USA. Mukkaw Bay lies in the North Temperate Zone (49^o N). The location was an intertidal zone and had a community typical of rocky shores in that area. Robert Paine conducted his experiment by designating some sections of the location as control sites and some as experimental sites. Both the control and experimental sites had similar conditions prior to the experiment. He then removed the top predator from the experimental sites. The top predator in Paine's experimental ecosystem was the predatory starfish *Pisaste*r spp. Pisaster preys on the Mussel *Mytilus californicus* and on the predatory whelk *Thais* spp. It also preys on other species including bivalves, limpets, barnacles and chitons. After the removal of the top predator *Pisaster*, he recorded the changes that occurred in both the experimental and the control plots over a period of 2 years. His findings showed that invertebrate species diversity remained constant at 15 in the control sites. In contrast, diversity within the experimental sites declined with a loss of 7 species. Could this loss be attributable to the suppression of competitive exclusion as the hypothesis proposes or was it due another cause? To answer this question the investigation must go further to look for evidence of competition. In other words, we must look for the interaction between biotic community and resource supply (two of the interactive controls in our framework).

The most common limiting resource in the rocky intertidal zone, such as Mukkaw Bay, is space. Within 3 months of the removal of *Pisaster*, the barnacle *Balanus glandula* occupied 60% to 80% of the available space created by the removal. By the end of one year of the experiment, the mussel *Mytilus californicus* and the barnacle *Pollicipes polymerus* had completely displaced *B. glandula*. Furthermore, there was a drastic decline in benthic algae and the species that fed on them had disappeared. Sponges also declined in number and the species that fed on sponges had declined in number. By the end of the fifth year of experimentation, experimental sites were dominated by just two species; *M. Californicus* and *P. polymerus* while control sites recorded no major changes

Species such as the predatory starfish Pisaster*,* whose feeding activities have such disproportionately large impacts on community structure, are known as keystone species. Although the keystone species effect has been demonstrated in many ecosystems around the world, further evidence from a wider geographical range is needed in order to fully understand the phenomenon. It is therefore a potential area for further investigation that may be considered by prospective research students.

The Species-Time Hypothesis

According to this hypothesis, gain in species diversity in any ecosystem is a factor of time. In other words communities will tend to gain more species as they become older. This may explain where species diversity is higher in tropical ecosystems that in temperate ones. A way to test this hypothesis is to measure diversity in a particular species from a range of communities the same biome with differing evolutionary ages. In this way confounding effects from other environmental conditions are reduced or eliminated. A good example of this kind of study was conducted by the paleoecologist H. J. B. Birks in Britain. Birks (1980) studied the species diversity of insects on trees with different evolutionary ages. His study found a significant correlation between the richness of species on trees and the evolutionary age of the trees. Birks used pollen age to estimate the evolutionary age of the trees studied which he compared with bird species richness

Many other studies, similar, the one by Birks have since been conducted. Some of them seem to support, at least, a variation of the hypothesis. Some notable studies in this line include Kennedy and Southwood (1984) and Brändle and Brandl (2001). The species-time hypothesis appears, however, to be applicable to habitats only. A study by Albert *et al* (1990) compared species diversity across taxa using a variation of this hypothesis in which the researchers investigating whether diversity would be higher in evolutionarily older taxonomic groups. To test this they investigated helminth parasite species richness in vertebrate hosts. They expected to find higher richness in fish, which are the evolutionarily older lineage than in birds and mammals. Their study did not find a correlation between these parameters. Instead, they found that aquatic vertebrate hosts (regardless of taxa) had higher parasite species richness than terrestrial vertebrate hosts. Thus the species-time hypothesis is still an area of great ecological debate (Birks 1980; Boucot 1983; Kennedy and Southwood 1984; Bush, Aho and Kennedy 1990; Price 1997; Brändle and Brandl 2001). It is therefore an interesting prospective area for the potential research student.

The Species-Area Hypothesis

According to this hypothesis species diversity should increase as the geographical area being considered increases. The rationale for this idea is illustrated in Figure 6.7. The species-area hypothesis has been put forward as a possible explanation for why species diversity is higher in the equatorial zone of the earth than at the polar zones. The equatorial zone covers a much larger geographical area than the polar zones.

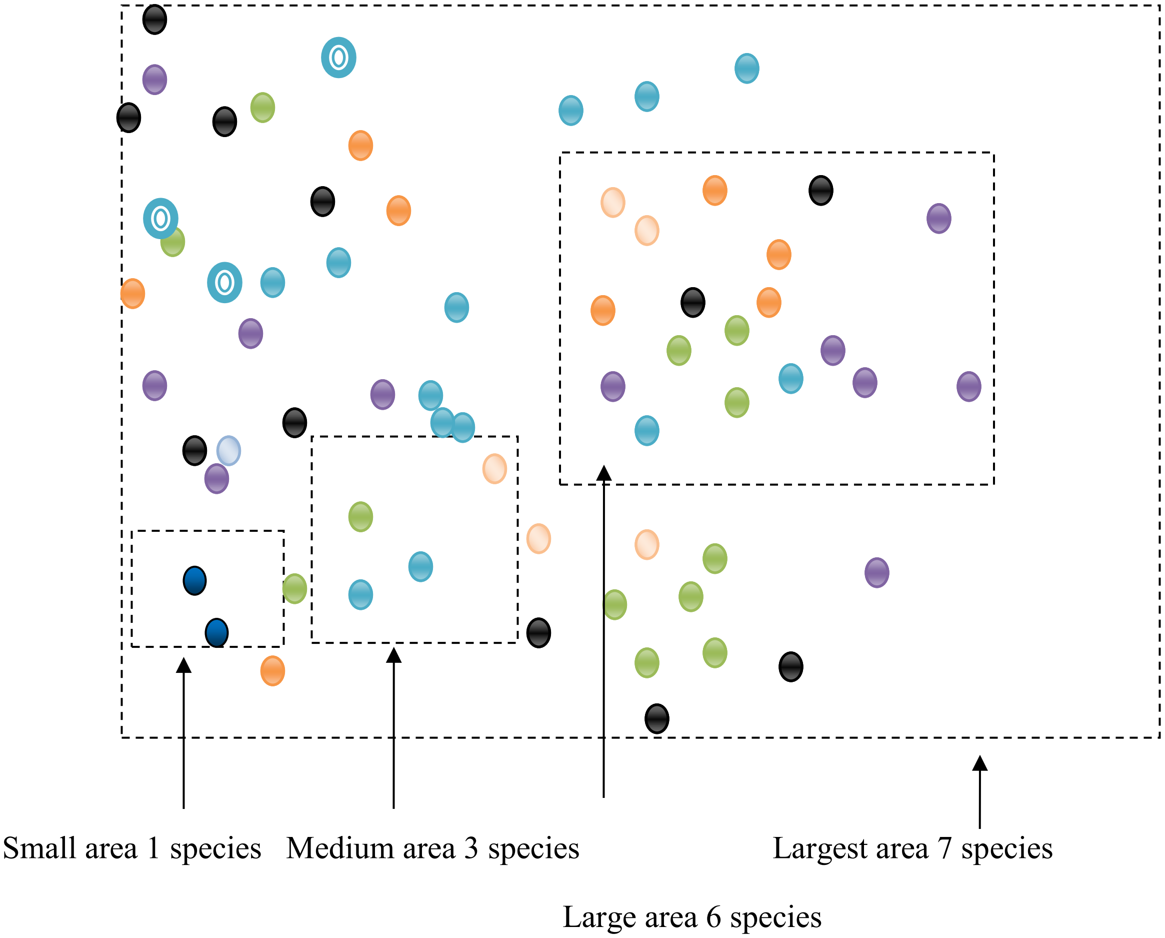


Figure 6.7: The Species-Area Hypothesis. Based on MacArthur and Wilson (1967)

The Species - Energy Hypothesis

The species-energy hypothesis proposes that ecosystems that receive high inputs of solar energy should have higher species richness than those with lower levels. The logic is that high solar radiation together with moisture availability should lead to higher primary productivity. High primary production makes more food available to support higher numbers of herbivores which in turn promotes larger numbers and diversity of predatory, parasitic and scavenger species. The hypothesis seems to be supported in terrestrial but not aquatic ecosystems. Many studies have shown a positive correlation between higher evapotranspiration rates and higher species richness (Currie, 1987). In aquatic ecosystems, however, there are several examples of ecosystems in which productivity is low but species diversity is high and vice versa. A good example is the area of the Pacific Ocean off the coast from Ecuador where productivity is low but species richness is high. Another example can be seen in situations where large inputs of nutrients resulting from pollution (as in the case of eutrophication) leads to higher productivity but low species diversity.

6.4. DISTURBANCE AND SUCCESSION

A disturbance is defined as an event that changes a community by removing organisms or altering resource availability. Disturbance can be caused by natural events such as floods, fires, droughts and hurricanes. Disturbance can also result from human activities. Disturbance can be beneficial or harmful to ecosystems. The obvious significance of disturbance to ecosystem functioning makes it a major area of ecological research interest. Some of the key areas of focus relate to the resistance, resilience and stability of ecosystems under disturbance. Other areas relate to the recovery of ecosystems after disturbance. With regards to ecosystem recovery after a disturbance, ecologists are particularly interested in a phenomenon known as ecological succession. In the next subsections we review each of these aspects of disturbance.

6.4.1. Resistance, Resilience and Stability

Ecosystem stability is defined as the persistence of an ecosystem despite the disturbance it is subjected to. Stability can result from resistance to disturbance or from resilience under disturbance. Resistance is when an ecosystem is able to maintain its structure and function despite being subjected to disturbance. Resilience, on the other hand, is the ability of an ecosystem to return to its former state after disturbance. The concept of ecosystem resilience is closely related to that of ecological succession since it is through this latter process that communities or ecosystems recover.

6.4.2. Ecological Succession

Ecological succession is the sequence of community changes that take place after a disturbance. Succession can be a primary or secondary. Primary succession occurs when disturbance is so severe that all the biotic legacies in the geographical location of interest have been completely wiped out. In that situation propagules must immigrate into the location from elsewhere. Primary succession usually occurs in situations where disturbance leads to the creation of new substrates such as during volcanic eruptions and glaciation. Some of the best documentation of what happens during primary succession is from these two types of activities.

Secondary succession, on the other hand, is the successional sequence that occurs in cases where disturbance does not lead to the complete removal of the existing substrate. In secondary succession, the geographical location in question retains some of its legacy of biotic propagules. For example, when part of a forest is cleared of trees, vegetation growth in the gap created undergoes secondary successional changes.

There is a great deal of debate between ecologists about what happens during succession. The debate started almost right from the beginning when the American ecologist Frederick Clements first put forward his theory about how it happens (Clements, 1905). Clements postulated that every geographical location has what he referred to as a climax community which if left undisturbed for long enough it ultimately returns to. According to this hypothesis, successional changes are predictable for locations and will go through a series of stages known as seral stages until finally a climax community which is characteristic of that location is reached. Under this model of succession, a disturbance may force a backward shift to a previous seral stage but the process of recovery to the climax community simply then picks up from there again. Clements' model of ecological succession perceived the community as a group of closely interlinked species that are so closely linked that they function almost as a "superorganism". To that extent the tendency to return to a climax community is like homeostasis in individual organisms. This view of succession is therefore based on the equilibrium model of how ecosystems work.

Like all models in science, Clements' views were not universally accepted. In 1926, another American ecologist Henry A. Gleason wrote a paper (Gleason, 1926) presenting a rival "individualistic" model to Clements' holistic model. In his model, Gleason argued that changes could be explained by random spreading and establishment by individual plant species and not by integrated action of a combination of species.

The Clementsian model of succession was based on the mechanism of Facilitation. In his model the first seral stage made up of pioneer species modify the habitat making it possible for the establishment of the second seral stage which in turn modifies the environment to make it possible for the third seral stage to arise. Facilitation continues until the climax community is ultimately attained. Gleason's alternative model suggests that possibility of other mechanisms alternative to or in addition to facilitation. In 1977 Joseph Connell and Ralph Slatyer proposed two additional mechanisms (inhibition and tolerance) involved in the process of succession. They proposed that successional change does not take place only through facilitation but could take several paths are illustrated in Figure 6.8. In effect, Connell and Slatyer's proposal is that there are actually three models of succession: the facilitation model, the tolerance model and the inhibition model.

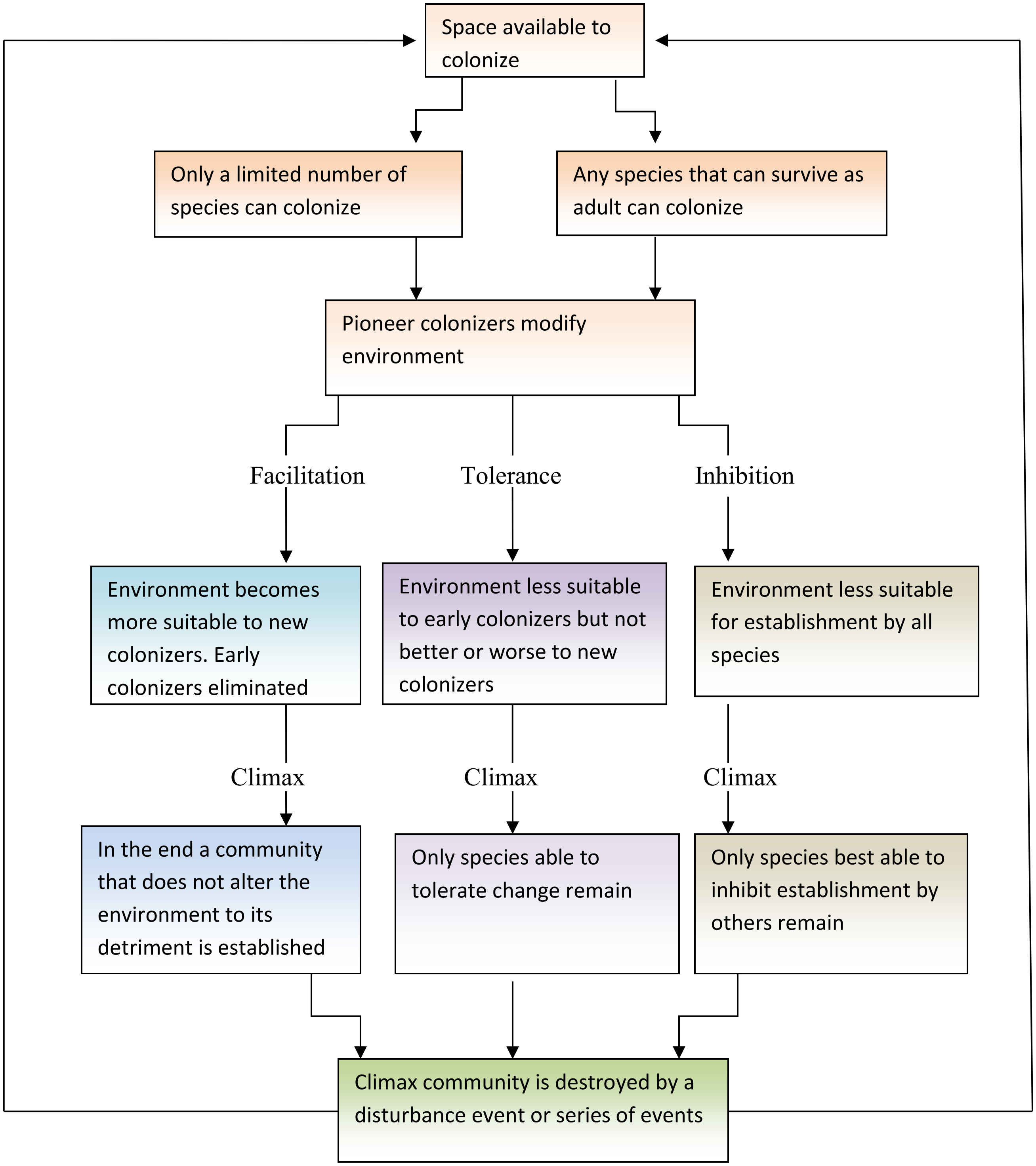


Figure 6.8: Models of ecological succession (based on Connell and Slatyer, 1977)

The Facilitation Model

This is the Clementsian model. It argues that first species to colonize, the pioneer species, modify the environment making it possible for new species to colonize and eliminate them through competition. This process is then repeated by the second seral group, followed by the third until a climax community is reached could only be removed by a disturbance. In other words stability is only achieved when climax is reached. One of the criticisms of the facilitation model is that it is 'group selectionist'. Species modifying the environment in such a way that they are eliminated appears not to be compatible with evolutionary theory

The Tolerance Model

In the facilitation model, there are specific geographic climax community regions and, in each of these, only a few species are capable of acting as pioneer species. The tolerance model argues that pioneer stage colonizing is not limited to just a few species. Instead a wide range of species propagules (including those from disturbed climax community) are present right from the pioneer stage. The model argues that pioneer species do not modify the environment to make it possible for new species to colonize. In other words, no facilitation takes place; instead the species that survive and establish themselves in each successional stage are those that are able to tolerate the conditions in the environment. Furthermore, the climax community (when successional change stops) is when populations of species that are not able to tolerate the environment are eliminated or reduced to an insignificant number.

The Inhibition Model

According to this model pioneer colonizers inhibit the establishment of other colonizers including late successional species. Over time, however, disturbance creates gaps within the community that allow other species to colonize the location as well. In this model the climax community is made of species that are able to survive longest in the community despite the disturbance regime during the time.

The debate about how successional change happens in ecosystems still continues and provides interesting research opportunity for the prospective research student.

6.4.3. The Intermediate Disturbance Hypothesis

One of the most interesting and researchable hypotheses in systems ecology is the intermediate disturbance hypothesis (IDH). This hypothesis argues that intermediate levels of disturbance should be beneficial to ecosystems. In other words it should promote the characteristics that help an ecosystem maintain its integrity; such as resistance, resilience and stability. IDH was first put forward by Joseph Connell (Connell 1978; Huston 1979). Since then, there has been a considerable body of research examining the effects of disturbance on species diversity. Much of this research focuses on testing the IDH. Predictions of the IDH are based on the logic that at high levels of disturbance, species diversity will be low because r-selected species that quickly colonize and reach maturity are able to survive. In contrast, at low disturbance frequency, species diversity is expected to be low, because competitively dominant K-selected species exclude all other species. At intermediate levels of disturbance species diversity is high because competitive exclusion is reduced since most species are not able to reach their maximum biotic potential. the relationship between species diversity and disturbance is illustrated in Figure 6.8.

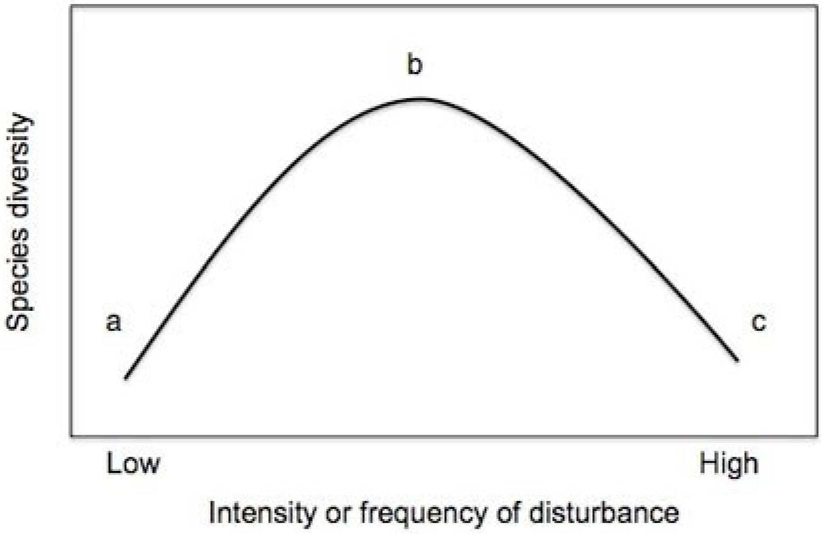


Figure 6.8: The intermediate disturbance hypothesis (IDH)
(A) Species diversity is low at low disturbance frequency because of competitive exclusion. (B) Species diversity is higher at intermediate disturbance frequency due to a mix of good colonizer and good competitor species. (C) Species diversity is low at high disturbance frequency because only good colonizers or highly tolerant species can persist.

Chapter 7: Engineering Concepts in Ecosystems Ecology

7.1 INTRODUCTION

As mentioned in chapter 3, the development of the concept of an ecosystem was deeply influenced by Systems Analysis. Consequently, it was only a matter of time before ecosystems started to be studied using the analytical methods of engineering. Systems analysis, (which really took off after World War II) conceived complex systems as interconnected components with feedback loops that stabilized the system and kept it in equilibrium. This type of thinking was particularly suited to the thoughts that had been festering in ecology for some time. For example, F.E. Clements' hypothesis about self-organization in plant communities was already being debated (Clements 1905, 1915). Similar thoughts about animal communities had also been put forward by the English animal ecologists Charles Elton. Elton (1927) was the first to describe the role of an animal in the community (it's niche) in terms of what it eats. He introduced the concept of the food chain and in so doing paved the way for the study of how energy flows and nutrients are cycled in the ecosystem. By 1935, A.G. Tansley had used the term ecosystem and the stage was fully set for the analysis of ecosystems from an engineering perspective.

One of the early pioneers in the use of systems analysis in ecosystem study is the American limnologists G. Evelyn Hutchinson. Hutchinson was strongly influenced by Charles Elton's ideas and was also familiar with the work of the Russian geochemist Verdansky who described mineral fluxes between soil and plants. This background, along with Hutchinson's familiarity with other concepts such as Liebig's Law of the Minimum, led him to suggest that the productivity of algae in a lake must be limited by the resources available to them in that lake and that algal productivity must in turn limit the productivity of other organisms that depend on them.

Another pioneer in the field of ecosystem ecology, whose ideas were influenced by the systems analysis paradigm, was Raymond L. Lindeman. Lindeman introduced the concept of using energy flow through a system as a currency to quantify the roles of organisms in trophic dynamics. Based on this concept, organisms may be classified as primary producers, consumers or decomposers. Primary producers (e.g. green plants) harness solar energy. This energy is then transferred in chemical form to consumers and decomposers within the system. Lindeman used his knowledge of the laws of thermodynamics to argue that some energy is lost at each trophic level as a result of respiration. The consequence of this is that the productivity of primary producers (which is the determinant of the potential biomass available for consumption) constrains the quantity of consumers that an ecosystem can support. Lindeman's work was so pioneering that his paper was initially rejected for publication. The paper was, however, published later (unfortunately after he had passed away at a tender age of 27 years).

The work of Raymond Lindeman together with those of Hutchinson paved way for a new generation of system ecologists. Foremost in this group were the brothers Eugene. P. Odum and Howard T. Odum. Both ecologists were students of G. E. Hutchinson. In the next sub-section we introduce Howard Odum's pioneering work and how it fully brought the engineering perspective into ecology

7.2 THE ECOSYSTEM FROM ENGINEERING PERSPECTIVE

The concept of an ecosystem can be said to have its roots from the holistic school of thought. The holistic approach is based on the view that mechanisms and processes can best be understood if studied from perspective of their outcomes. The alternative view, which is known as the reductionist approach contends that things are best understood by breaking them into small parts and studying the component parts continuously until the most fundamental components are discovered and understood. The holistic approach to the study of ecology argues that the primary value of nature is how its components integrate to produce the essential ecological services that make it possible for life to be sustained on earth. The holistic approach to the study of nature is particularly amenable to the application of engineering principles because of its emphasis on the end result. This is because engineers, fundamentally, think differently from scientists. Scientists are interested in how things work. Engineers on the other hand are interested how to build things. A scientist may be interested in ecosystems in other to know how they function. An engineer's interest in ecosystems is to understand how the system works in other to use the knowledge to engineer solutions to problems.

The first person to translate the concept of the ecosystem into engineering use is Howard T. Odum. H.T. Odum was the first to use the term "community engineering" to refer to the manipulation of species within biotic communities to achieve engineering goals (H. T. Odum and Hoskin, 1957). By the 1970s, the machine analogy inherent in systems analysis had become a major paradigm in ecosystems ecology and could be seen in the works of many ecologists (Odum, 1971; Holling, 1973; Waide and Webster 1976). The perception of the ecosystem as some form of machine meant that systems ecologists could now use a wide range of analytical tools already available to engineers to address the enormous complexity of natural systems. Lindeman's use of energy as the currency for determining the efficiency of ecosystem function was highly influenced by this perception. H. T. Odum built on the work of Lindeman to develop a new concept of the ecosystem based on the transfer of energy. In his pioneering work (H.T. Odum, 1957) Odum produced the first sets of ecosystem diagrams using symbols from the energy circuit language. An example of how these symbols have been used to depict ecosystems is given in Figure 7.1. The symbols used in these types of diagrams are explained in Box 7.1

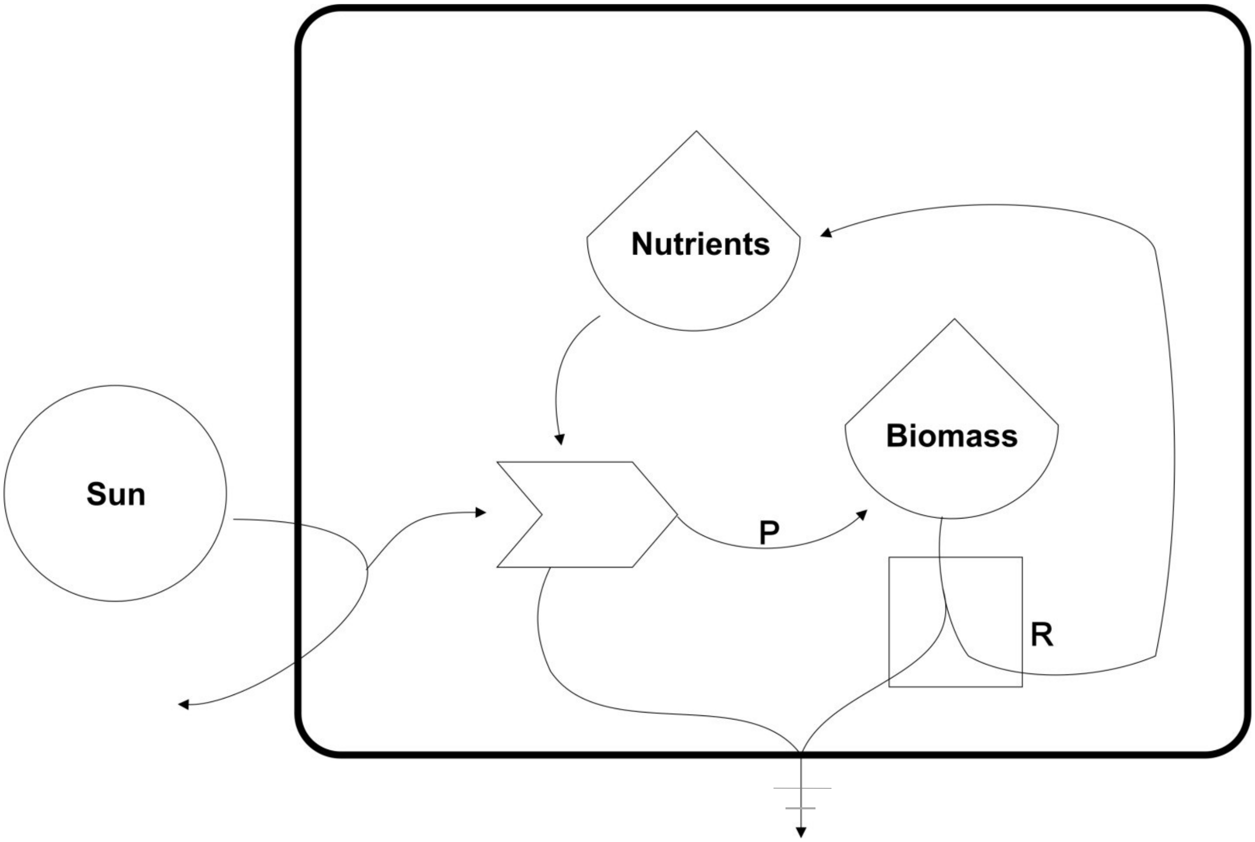
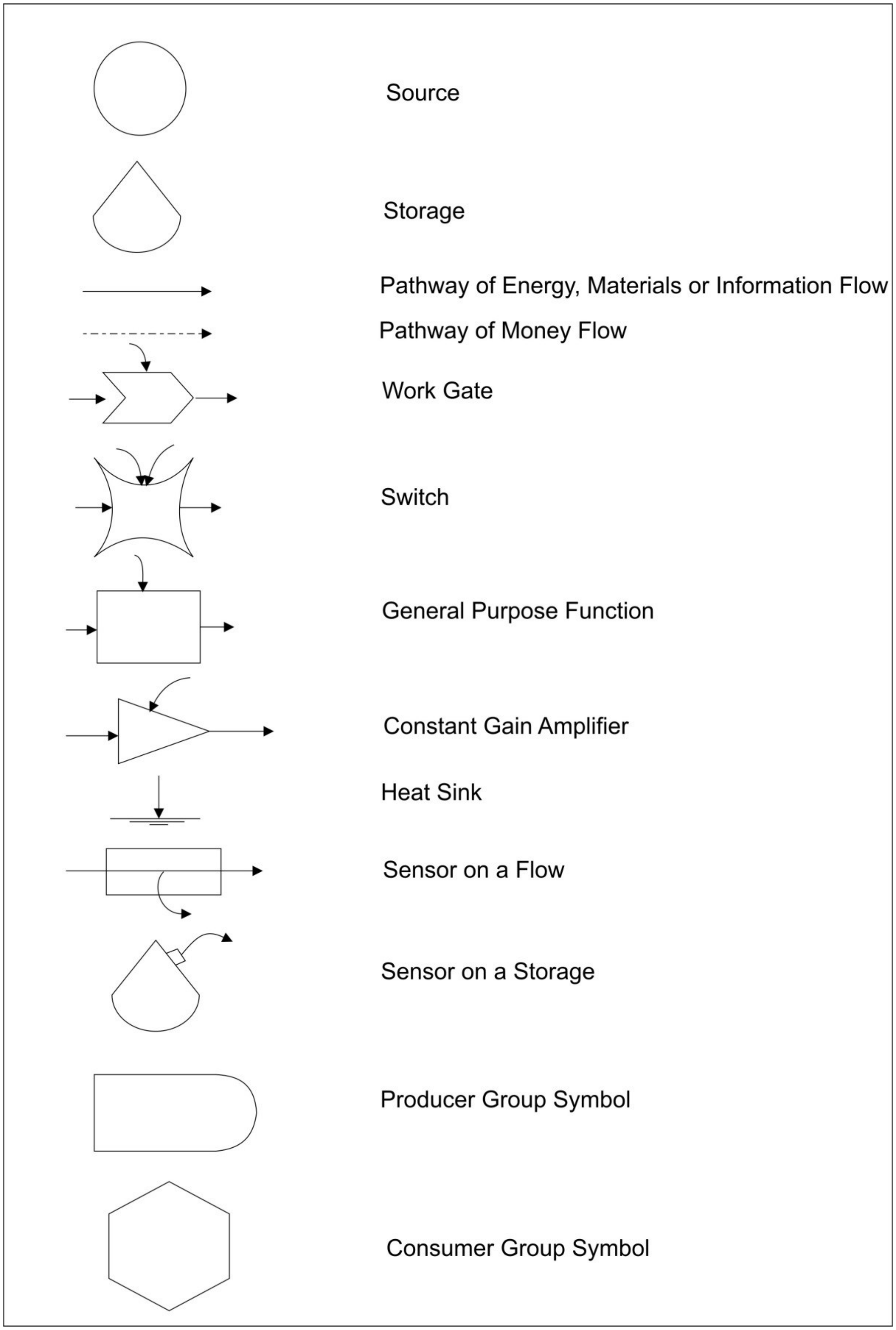


Figure 7.1: Basic P-R Model of the Ecosystem. P stands for primary production and R for community respiration. (From: Kangas, 2005)



Box 7.1: Symbols from the energy circuit language. (Source: Kangas 2004)

7.3 THE FIELD OF ECOLOGICAL ENGINEERING

The term ecological engineering was coined by Howard T. Odum in the 1960s. The idea of a discipline of ecological engineering was a natural progression from the paradigm of the ecosystem as integrated system with interconnected components. It was based on the recognition that the engineering perspective can be leveraged to achieve better understanding of ecological systems and in so doing attain greater harmony between humans and nature.

As mentioned in the introduction to this chapter, the works of A.G. Tansley, C. Elton, G. E. Hutchinson and R. Lindeman blazed the trail for this approach. H.T. Odum is, however, regarded as the father of modern day ecological engineering. In one of his evolving definitions of the concept, he defined ecological engineering as "the environmental manipulation by man using small amounts of supplementary energy to control systems in which the main energy drives are still coming from natural sources (Odum *et al*, 1963). An early summary of H.T. Odum's ideas is presented in one of the chapters in his book on the energy systems theory (H.T. Odum 1971). The ideas presented in that source were presented under headings most of which like "Life support values of diversity" are still on the agenda of ecological engineering some 40 years later. Since the pioneering work of H.T. Odum, ecological engineering has gradually progressed in the general direction that focuses on the use of engineering approaches to manipulate ecological systems to achieve specific engineering goals or for the purposes of research to better understand these systems. It is worth noting that parallel but separate developments towards the development of the discipline in China and in central Europe have both converged towards similar goals with those in the West that we have so far been describing. In central Europe the ecological engineering perspective has developed into a discipline referred to as ecotechnology. Ecotechnology has been defined as "the use of technological means to for ecosystem management based on deep ecological understanding, to minimize the costs of measures and their harm to the environment (Uhlmann, 1983; Straskraba and Gnauck, 1985; Straskraba, 1993). In the West, Teal (1991) has defined ecological engineering as the use of "ecological processes within natural or constructed imitations of natural systems to achieve engineering goals. Mitsch and Jorgensen (2003) have argued that the ecological engineering involves creating and restoring sustainable ecosystems that have value for both man and nature. We this perspective in view, they consider the goals of ecological engineering and ecotechnology to be

1. The restoration of ecosystems that have been substantially disturbed by human activities such as environmental pollution or land disturbance and
2. The development of new sustainable ecosystems that have both human and ecological value

They argue that ecological engineering is engineering in the sense that "it involves the design of the natural environment through quantitative approaches [that rely on basic science]. It is technology whose primary tool is the self-designing ecosystem. It is biology in the sense that the components are all of the biological species of the world"

Mitsch and Jorgensen (2003) identify five basic concepts that collectively distinguish ecological engineering from other approaches to that address environmental problems using engineering approaches. These concepts are that ecological engineering

(i) is based on the self-design capacity of ecosystems
(ii) can be the acid test of ecological theories
(iii) relies on system approaches
(iv) conserves non-renewable energy sources and
(v) supports biological conservation

The concept of self-design is related to the concept of self-organization. Self-organization is the property of systems that enables them to reorganize themselves given an environment that is inherently unstable and non-homogeneous. Self-organization is a property that is well suited ecosystems in which state factors are constantly pushing the system towards change. From engineering perspective, systems can be organized in one of two ways. They organized through imposed organization or they can self-organize. Imposed organization is the top-down control or external influence that can be imposed on the system by an engineering intervention. On the other hand, the system can self-organize itself in which case the contribution of engineering is to understand this process, to learn from it and to recreate or facilitate it when needed. Self-organization develops flexible networks that have a better potential to adapt to change. It is for this reason that designing systems for self-organization is so much more suitable for ecosystems management. Self-design is the application of self-organization in the design of ecosystems. For example, in the context of ecosystem development, if an ecosystem is engineered in such a way that it can allow "seeding of enough species and their propagules such a system will have more potential to self-organize by optimizing its design by selecting for the assemblage of species that are best adapted for the existing conditions within the system. That is what is meant by self-design

Ecological engineering also provides a good platform for putting ecological theory to test. The best way to check the validity of the predictions of a model is attempt recreate the theorized situation in real life and to see if the outcomes predicted do actually occur. To this end ecological engineering becomes the acid test for the conjectures of ecological theoreticians. It is therefore a tool for fundamental ecological research.

A third concept that distinguishes ecological engineering from other engineering approaches to environmental problems is that it is based on the system approach. In ecological engineering the environmental problem being addressed is viewed from a holistic perspective with effects on all components of the ecosystem taken into account during design. Ecological engineering therefore relies on system tools, such as ecosystem modelling, that take into consideration complex links between components within the system. Not all engineering approaches to environmental problems adopt this approach hence the distinction in literature between environmental engineering and ecological engineering.

Another difference between ecological engineering and other engineering approaches to environmental problems is that it is based on the concept of the conservation of non-renewable resources. Many environmental engineering solutions rely on the use of non-renewable fossil fuel for energy. Ecological engineering approaches are based on the concept of self-design. This means ecologically engineered ecosystems are expected to constantly self-organize in order to remain self-sustaining using solar inputs of energy into the system

Finally ecological engineering revolves around the concept of ecosystem conservation. Ecological engineering is based on the use of ecosystem processes as the means to achieve engineering goals. The consequence of this is that design must be done in such a way that it conserves the essential ecosystem processes rather than undermine them. To this end pollution, habitat destruction and fragmentation and other forms of disturbances that are harmful to ecosystem functioning are incompatible with the ecological engineering approach.

Finally, as the world is faced with ever increasing environmental challenges, ecological engineering offers a very useful tool for a better understanding of ecosystem function and for the development of technologies for the sustainable use of natural resources and the preservation of the essential ecological services on which life on earth depends.

7.4 MATHEMATICAL MODELLING OF BIOTIC MECHANISMS

A key concept corollary to evolutionary theory is that natural selection will tend to lead to the domination of traits that enable organisms to obtain energy in the most efficient ways possible within the constraints imposed on them by the environment. This concept of optimization is pervasive in the analysis of ecological systems and forms the basis for ecological modelling frameworks such as the Optimal Foraging Theory. The premise of optimal foraging theory is that natural selection will favor animals that possess traits that enable them to maximize energy intake rates and therefore this phenomenon should be widespread in nature. The logic of this argument is rooted in the principle of allocation which states that energy allocated for one function is not available for another and therefore the more energy there is at the disposal of an organism, the more it is able to perform all its life functions effectively. For example, energy that is used by a territorial animal to defend territory against conspecifics is not available for reproduction. Hence individuals within the same species who have a higher rates of energy intake will be able to allocate more to reproduction and hence produce more offspring that those with lower rates of energy.

Optimal foraging theory is one of the phenomena of ecology that has been most subjected to mathematical modelling. Mathematical analysis is used to predict the outcomes expected under various scenarios if organisms were attempting to forage optimally. As an example let us consider a model used by Earl Werner and Gary Mittelbach. Werner and Mittelbach (1998) modelled the rate of intake of energy for a predator feeding on one, two and several species as follows:

For a predator feeding on a single species the rate of intake of energy can be represented as:

$$\frac{E}{T} = \frac{N_{e1}E_1 - C_s}{1 + N_{e1}H_1} \quad \text{------------------------ Equation 1}$$

Where N_{e1} = number of prey type 1 encountered per unit time

E_1 = energy gained by feeding on an individual of prey species 1 minus the cost of handling

C_s = cost of searching for the prey

H_1 = time required for handling an individual of prey species 1

For a predator feeding on two types of prey (Prey species 1 and Prey species 2):

$$\frac{E}{T} = \frac{(N_{e1} - C_s) + (N_{e2}E_2 - C_s)}{1 + N_{e1} + N_{e2}H_2} \quad \text{---------------------- Equation 2}$$

Equation 2 is an extension of equation 1 in which N_{e2} (the encounter of prey species 2), E_2 (the energetic return from feeding on prey species 2 and H_2 (the handling time for prey species 2) have been added. C_s (cost of searching has been assumed to be the same for prey species 1 and prey species 2.

For a predator feeding on several prey species, the rate of intake of energy is given as:

$$\frac{E}{T} = \frac{\sum_{i=1}^{n} N_{ei}\ E_i - C_s}{1 + \sum_{i=1}^{n} N_{ei}\ H_i} \quad \text{------------------------------------ Equation 3}$$

Equations 1, 2, and 3 give the estimate of the rate of intake of energy for one prey species, two prey species and several prey species respectively. However, since we are interested in whether the predator is feeding at a rate that maximizes its intake of energy, this is not the end of the matter. The next process is to use optimization analysis to predict what should happen under various scenarios and then either to create these scenarios in experimental settings or to try to find them in natural settings and compare these outcomes with those predicted by the model. Using the model they developed, Werner and Mittelbach predicted the following:

To maximize its rate of energy, the predator will feed only on prey species 1 if the rate of intake when feeding on both species 1 and species 2 is less than that when feeding on species 1 alone. That is if:

$$\frac{N_{e1}E_1}{1+N_{e1}H_1} > \frac{N_{e1}E_1 + N_{e2}E_2}{1+ N_{e1}H_1 + N_{e2}H_2}$$

However, the predator will feed on both prey species 1 and prey species 2 if the rate of intake of energy for doing that is greater than for feeding on prey species 1 alone. That is if

$$\frac{N_{e1}E_1 + N_{e2}E_2}{1+ N_{e1}H_1 + N_{e2}H_2} > \frac{N_{e1}E_1}{1+N_{e1}H_1}$$

Mathematical models such as the one illustrated above are useful because they provide the theoretical framework for the conduct of empirical research. They help field ecologists to design field studies to test their predictions. Where field data contradicts the predictions of the model, the assumptions of the model are refined to more closely reflect the reality in nature. In this way models evolve; becoming more robust with time. As a result of this process mathematical models in use today have come a long way from the first models developed. For example, early models of optimal foraging focused solely on the maximization of energy intake rates. They did not include the fact that an animal must try to avoid predators while it is searching for and handling food items. The models also failed to take into consideration the fact that certain food items although having the potential to provide the animal with more energy intake per unit effort may actually be avoided because they contain toxins. Although there is much more to do, today models have incorporated many aspects that were not considered in early models. Mathematical modelling is therefore a very important tool for the study of ecological systems and will continue be of significant heuristic value for a long time. There is no doubt that the adoption of the engineering perspective for the study of ecosystems played a great part in this development.

7.5 ORGANISMS AS ECOSYSTEM ENGINEERS

The concept of organisms acting as ecosystem engineers was first proposed by Jones, Lawton and Shachak (1994). This concept, which was highly influenced by systems analysis perspective, was introduced as attempt to try and coalesce the already known fact that some organisms make physical changes (engineer structures) within the environment in which they live. Such structures usually profoundly affect the functioning of the ecosystem in which they are built. For example, beavers build dams in the environment in which they live. These dams can significantly affect river flow creating a range of associated changes in the environment. Beavers, termites and many other organisms that build biogenic structures are therefore referred to as ecosystem engineers. This term is not to be confused with ecological engineers (who are humans who use engineering techniques to change, reproduce or induce ecosystem processes). It is also not to be confused with environmental engineering which is the use of engineering techniques to solve environmental problems using non-renewable energy sources.

In their pioneering paper Clive Jones and his colleagues (Jones *et al*, 1994) defined ecosystem engineers as organisms that “directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic and abiotic materials. In so doing they modify, maintain and create habitats”. According to this definition an effect may only be considered to be an ecosystem engineering effect if it arises from physical changes created by the actions of the organism. By this definition, trophic interactions involving the consumption or provision of tissue are not considered to be engineering actions. Based on their definition, Jones *et al* (1994) classified ecosystem engineers as either autogenic or allogenic in their effects on the environment. Autogenic engineers change the environment through their own physical structures while allogenic engineers do so by transforming living or non-living material from one physical state to another through mechanical or other means. Since this publication, a great deal of debate has been going on as to what exactly qualifies as an ecosystem engineering effect on the environment. As a result of these debates, several frameworks have been proposed for the understanding ecosystem engineering by organisms. Two recent frameworks, one by Clive Jones and colleagues (Jones *et al*, 2010) and another by Sarah Berke (Berke, 2010) are particularly of interest. Figure 7.2 summarizes the framework by Jones et al, 2010. According to this framework a key criterion for regarding an organism as an ecosystem engineer is that it creates a structural change which leads to an abiotic change which in turn creates biotic change. Structural change can be allogenic or autogenic. The framework therefore emphasizes the organism carries out structural change before it can be regarded as an ecosystem engineer. By this definition, therefore, the most important ecosystem engineers on our planet today are the human species; but they are by no means the only species of ecosystem engineers.

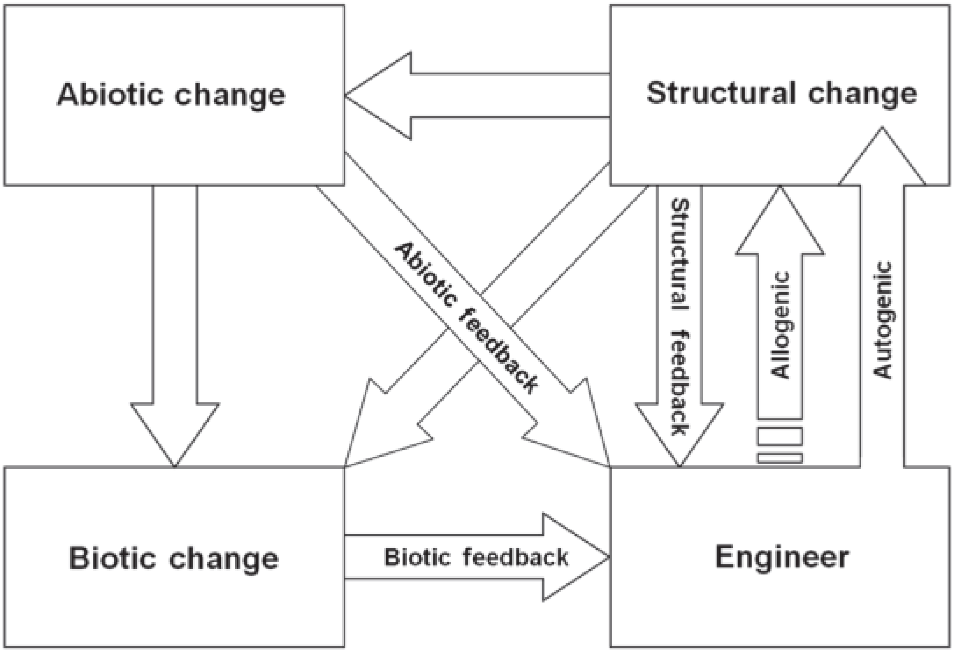


Figure 7.2: A framework for understanding ecosystem engineering activities by organisms in ecosystems. The figure shows the cause/effect relationships representing an engineered system. The allogenic relationship represents physical structures constructed by the engineer while the autogenic relationship represents actions of the engineer on both the living and non-living components of the ecosystem. (Source: Jones *et al*, 2010)

In the same year that Clive Jones and his colleagues proposed the framework highlighted above a paper was published by Sarah Berke (Berke, 2010) in which she proposed four functional categories of ecosystem engineers each with its associated suite of models (Figure 7.3)

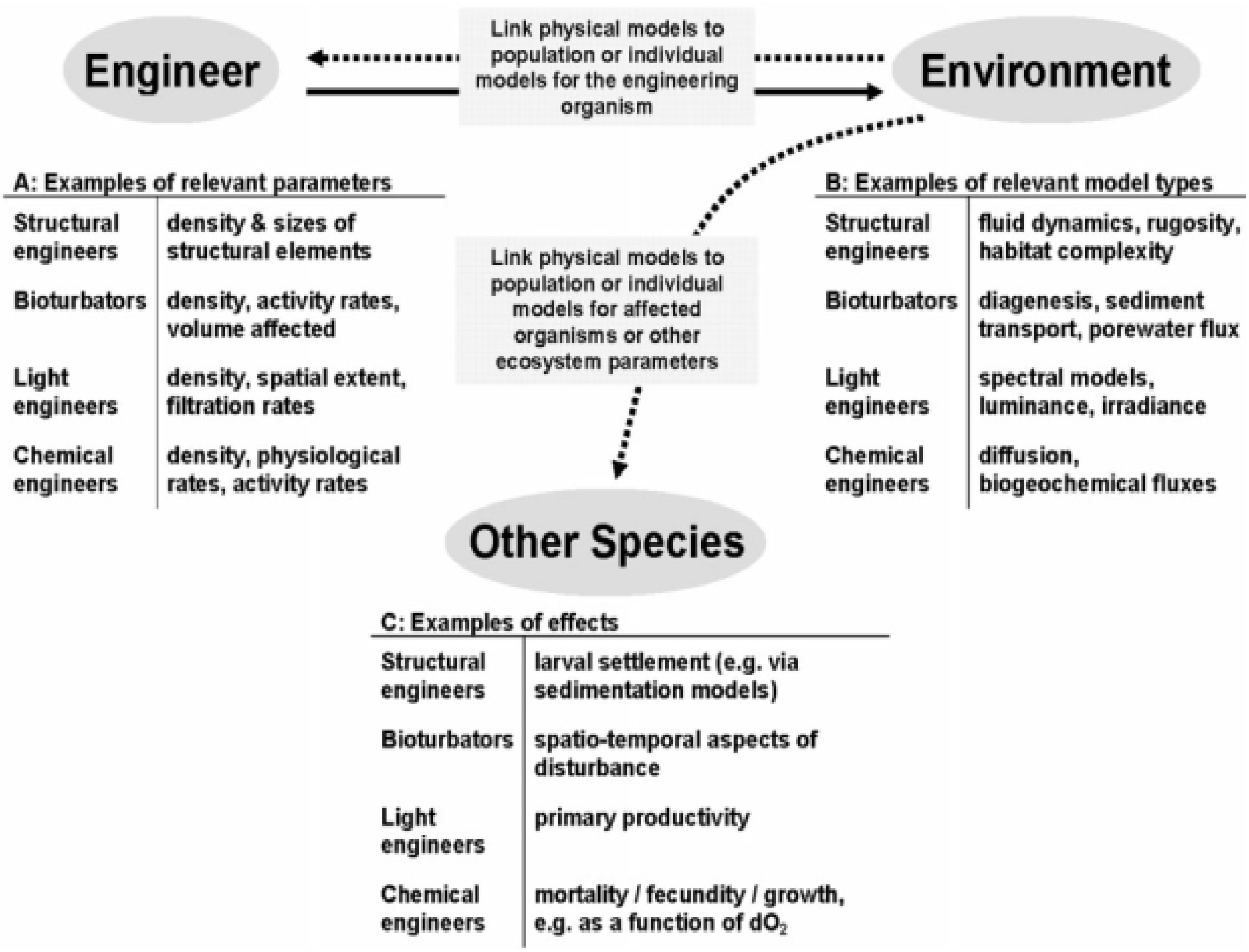


Figure 7.3: A conceptual framework for ecosystem engineering models based on linking engineer populations to other species via their physical effects (Source: Berke, 2010)

Berke’s classification of ecosystem engineers is process-based as opposed to the outcome-based classifications that have been used in the past. One of the arguments that she used in support of the process –based approach is that an outcome-based classification will lead to an intractable number of categories. She gave an example with infaunal polychaetes which she found to affect flow, particle deposition, habitat heterogeneity, local abundance, local richness, local community composition, frequency of disturbance, mixing of sediments and the depth of oxygen penetration. For this and other reasons, Berke argues that process-based categories are more amenable to modelling than those based on outcomes. She went on to suggest a roadmap for using process-based categories to model ecosystem engineering effects (Figure 7.3)

To illustrate modelling using process-based categories consider marine structural engineers whose actions influence fluid dynamics in the ecosystem. In such a case, fluid dynamics models can use information about the size and density of emergent structures to make predictions about physical parameters such as particle and larvae sedimentation rates

In conclusion, the concept of organisms as ecosystem engineers although still in its early stages of development, provides a useful framework of modelling of ecosystem processes and is a great opportunity for potential research students with strong mathematics backgrounds to contribute to greater understand of how ecosystems function.

G. E. Hutchinson

Raymond Lindeman

Howard Odum

Eugene Odum

References and Recommended Reading

Allen, E. B. and M. F. Allen. 1986. Water relations of xeric grasses in the field: interactions of mycorrhizae and competition. *New Phytologist* 104:559-71.

Agrawal, A. A., Ackerly, D. D. *et al*. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5, 145-152.

Allison, G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs* 74: 117-134

Amundson, R and H. Jenny, 1997. On a state factor model of ecosystems *BioScience* 48(8):536-43

Bazilevich, N. I., A. V. Drozdov, and L. E. Rodin. 1971. World forest productivity, its regularities and relationships with climatic factors. Pages 345-353 in Duvigneaud, P (ed). Ecology and Conservation. UNESCO. Paris. France

Bazilevich, N. I., Rodin, L. Ye., and Rozov, N. N. (1971). Geographical aspects of biological productivity. *Sov. Geogr. Rev. Transl*. 12: 293-317

Balvanera, P., Pfisterer, A. B. *et al*. 2006.Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9: 1146-1156

Berke, S. K. 2010. Functional groups of ecosystem engineers: A proposed classification with comments on current issues. *Integrative and Comparative Biology* 50(2):147-157

Birks, H. J. B. 1980. British trees and insects: a test of the time hypothesis over the last 13,000 years. *American Naturalist* 115: 600-605

Box, E. O. 1980. What determines the amount of leaf and total standing biomass of climax terrestrial vegetation? *Bulletin of the Ecological Society of America* 61(2):76

Broeker, W. E. 1970. Man's oxygen reserves. *Science* 168: 1537-38

Bruno, J. F., Fridley, J. D. *et al*. 2005. In *Species Invasions: Insights into Ecology, Evolution, and Biogeography*, eds. Sax, D. F., Stachowicz, J. J. *et al*. (Sunderland: Sinauer Associates,): 13-40.

Bruno, J. F., Stachowicz, J. J. *et al*. 2003. Inclusion of facilitation into ecological theory. *Trends In Ecology & Evolution* 18: 119-125

Bush, A. O., J. M. Aho, and C. R. Kennedy. 1990. Ecological vs Phylogenetic determinants of helminth parasite community richness. *Evolutionary ecology* 4:1-20

Cardinale, B. J. & Palmer, M. A. 2002. Disturbance moderates biodiversity-ecosystem function relationships: experimental evidence from Caddisflies in stream mesocosms *Ecology* 83:1915-1927

Cardinale, B. J., Srivastava, D. S. *et al*. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989-992

Carpenter, R. C. 1981. Grazing by *Diadema antillarum* (Phillips) and its effects on the benthic algal community. *Journal of Marine Research* 39:749-765

Carpenter, S. R. and J. F. Kitchell. 1988. Consumer control of lake productivity. *BioScience* 38:764-69

Carpenter, S. R. and J. F. Kitchell. 1993. *Trophic cascade in lakes.* Cambridge. England. Cambridge University Press.

Carpenter, S. R., Kitchell, J. F. & Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634-639.

Chapin, F.S., III, L. R. Walker, C. L. Fastie, and L. C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64:149-61

Chapin, F.S., III, P. A. Mason, and H. A. Mooney. 2002. Principles of Terrestrial Ecosystem Ecology, Springer, New York.

Chase, J. M. & Leibold, M. A. 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416: 427-430.

Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington. Publication 242.

Clements, F. E. 1936. The nature and structure of the climax. *Journal of Ecology* 24:252-84

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-23

Connell,J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In M. L. Cody and J. Diamond eds. *Ecology and Evolution of Communities*. Cambridge, Mass.: Harvard University Press.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302-1310

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661-96

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119-44

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. The Botanical Gazette 27:95-117, 167-202, 281-308, 361-91.

Dayton, P. K. 1972. "Toward an understanding of community resilience and the potential effect of enrichments to the benthos at McMurdo Sound." *Proceedings of the Colloquium on Conservation Problems in Antarctica*, ed. B. C. Parker. Allen Press.

De Moraes, C. M., W.J. Lewis, P. W. Pare, H. T. Alborn, and J. H. Tumlinson. 1998. Herbivore-infested plants selectively attract parasitoids. Nature 393: 570-573

Doak, D. F., Bigger, D. *et al*. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist* 151:264-276.

Dillon, P. J. and F. H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. *Limnology and Oceanography* 19:767-73

Dillon, P. J. and F. H. Rigler. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. *Journal of the Fisheries Research Board of Canada* 32:1519-31

Dobzhansky, T. 1950. Evolution in the tropics. *American Scientist* 38:209-21

Duffy, J. E. 2009 Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment* 7: 437-44.

Ehrlich, L.E. and A. H. Ehrlich, 1981. *Extinction: the Causes and Consequences of the Disappearance of Species.* Random House, New York

Eisener, T. and D. J. Aneshansley. 1982. Spray aiming in bombardier beetles: jet deflection by the Coanda effect. Science 215: 83-85

Elton, C. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. *British Journal of Experimental Biology* 2:119-63

Elton, C. 1927. *Animal Ecology*. London. Sidgewick & Jackson

Findlay, D. L. and S. E. M. Kasian. 1987. Plankton community responses to nutrient addition in Lake 226. Experimental Lakes Area, northwestern Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 44 (Suppl. 1):35-46.

Fisher, S. G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. *Environmental Management* 14:725-36

Forbes, S. A. 1887. The lake as a microcosm. *Bulletin of the Peoria Scientific Association.* Reprinted in the *Bulletin of the Illinois State Natural History Survey* 15 (1925): 537-50

Gause, G. F. 1934. *The struggle for existence.* Baltimore. Williams & Wilkins. Reprinted by Hafner Publishing Company. New York, 1969.

Gleason, H. A. 1926. The individualistic concept of the plant association. *Torrey Botanical Club Bulletin* 53: 7-26

Gleason, H. A. 1939. The individualistic concept of the plant association. *American Midland Naturalist* 21:92-110

Gotelli, N.J. and G.R. Graves. 1996. *Null models in ecology*. Smithsoniam Institution Press, Washington, DC.

Grier, C. C. and S. W. Running. 1978. Leaf area of mature coniferous forest: relation to a site water balance. Ecology 58:893-899

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169-1194

Grinnell, J. 1917. The niche-relationships of the California Thrasher. *Auk* 34:427-33.

Grinnell, J. 1924. Geography and evolution. *Ecology* 5:225-29

Gustafson, R. G., Waples, R. S. *et al*. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. *Conservation Biology* 21:1009-1020.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960. Community structure, population control, and competition. *The American Naturalist* 94:421-425.

Higuchi, T. 1983. The visual and spatial structure of landscapes. MIT Press. Cambridge Massachusetts USA.

Hilborn, R., Quinn, T. P. *et al*. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences, USA* 100:6564-6568

Hogetsu, K. and S. Ichimura, 1954. Studies on the biological production of Lake Suwa. 6. The ecological studies in the production of phytoplankton. *Japanese Journal of Botany* 14:280-303

Hughes, A. R., Byrnes, J. E. *et al*. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters* 10:849-864.

Hughes, A. R., Inouye, B. D. *et al*. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11**:**609-623.

Hughes, A. R. & Stachowicz, J. J. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences, USA* 101: 8998-9002

Huston, M. A general hypothesis of species diversity. 1979 *American Naturalist* 113**:** 81-101

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Symposium on Quantitative Biology* 22:415-27

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many different kinds of animals? American Naturalist 93: 145-159.

Hutchinson, G.E. 1961. The paradox of the plankton. *American Naturalist* 95: 137-45.

Ichimura, S. 1956. On the standing crop and productive structure of phytoplankton community in some lakes of central Japan. *Japanese Botany Magazine Tokyo* 69:7-16

Jenny, H. 1941. *Factors of Soil formation: A System of Quantitative Pedology*. McGraw-Hill New York

Jones, C. J., J. H. Lawton and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69(3): 373-386

Jørgensen, S. E. 1982. Energy and buffering capacity in ecological systems. pp. 61–72. In: *Energetics and Systems*. W. J. Mitsch, R. K. Ragade, R. W. Bosserman, and J. A. Dillon, Jr. (eds.). Ann Arbor Science, Ann Arbor, MI.

Jørgensen, S. E. 2000. The tentative fourth law of thermodynamics. pp. 161–75. In: *Handbook of Ecosystem Theories and Management*. S. E. Jørgensen and F. Muller (eds.). Lewis Publishers, Boca Raton, FL.

Jørgensen, S. E. (ed.). 2001. *Thermodynamics and Ecological Modelling*. Lewis Publishers, Boca Raton, FL.

Jørgensen, S. E. and F. Muller (eds.). 2000. *Handbook of Ecosystem Theories and Management*. Lewis Publishers, Boca Raton, FL.

Jørgensen, S. E., H. Mejer, and S. N. Nielsen. 1998. Ecosystem as self-organizing critical systems. *Ecological Modelling.* 111:261–68.

Kangas, P. C. 2004. *Ecological Engineering: Principles and Practice*. Lewis Publishers, CRC Press, Boca Raton

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich, 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636-638

Kimbro, D. L. & Grosholz, E. D. 2006. Disturbance influences oyster community richness and evenness, but not diversity. *Ecology* 87:2378-2388.

Kingsland, S.E. 1995. Modeling nature, 2nd ed. Univ. Chicago Press, Chicago, IL.

Jones C. G., J. H. Lawton and M. Shachak, 1994. Organisms as ecosystem engineers. *Oikos* 69(3):373-86

Jones C. G.,J. L. Guitierrez, J. E. Byers, J. A. Crooks,J. G. Lambrinos, and T. S. Talley, 2010. A framework for understanding physical ecosystem engineering by organisms. *Oikos* 119:1862-69

Laurenroth, W. K. and O. E. Sala. 1992. Longterm forage production of North American shortgrass steppe. Ecological Applications 2: 397-403

Lawton, J. H. 1994. What do species do in ecosystems? *Oikos.* 71:367–374.

Lawton, J. H. 1995. Ecological experiments with model systems. *Science.* 269:328–331.

Lawton, J. H. 1997. The role of species in ecosystems: Aspects of ecological complexity and biological diversity. pp. 215–228. In: *Biodiversity: An Ecological Perspective*. T. Abe, S. A. Levin, and M. Higashi (eds.). Springer. New York.

Lawton, J. H. 1998. Ecological experiments with model systems: the Ecotron facility in context. pp. 170–182. In: W. J. Resetarits, Jr. and J. Bernardo (eds.). *Experimental Ecology*. Oxford University Press, New York.

Lawton, J. H. and C. G. Jones. 1995. Linking species and ecosystems: Organisms as ecosystem engineers. pp. 141–150. In: *Linking Species and Ecosystems*. C. G. Jones and J. H. Lawton (eds.). Chapman & Hall, New York.

Levine, J. M., Adler, P. B. *et al*. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7**:**975-989

Liebig, J. 1840. *Chemistry in its Application to Agriculture and Physiology* Taylor & Walton, London

Lieth, H. 1975. Some prospects beyond production measurement: Comparative analysis of some biomass properties on the ecosystem level. In: Primary productivity of the Biosphere. Ecological Studies 14. H. Leith and R. H. Whittaker, eds. Springer-Verlag New York

Likens, G. E. (ed.). 1972. *Nutrients and Eutrophication: The Limiting-Nutrient Controversy. Special Symposia*, Vol. 1, American Society of Limnology and Oceanography, Inc., Lawrence, KS.

Likens, G. E. (ed.). 1989. *Long-Term Studies in Ecology, Approaches and Alternatives*. Springer-Verlag, New York.

Likens, G. E. 1992. *The Ecosystem Approach: Its Use and Abuse*. Ecology Institute, Oldendorf/ Luhe, Germany.

Likens, G. E., F. H. Bormann, R. S. Pierce, J. S. Eaton, and N. M. Johnson. 1977. *Biogeochemistry of a Forested Ecosystem.* Springer-Verlag, New York.

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

Loreau, M., Mouquet, N. *et al*. 2003: Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences, USA* 100:12765-12770

Loreau, M., Naeem, S. *et al*. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294**:**804-808

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112: 23-39

Lyons, K. G., Brigham, C. A. *et al*. 2005. Rare species and ecosystem functioning. *Conservation Biology* 19:1019-1024

MacArthur, R. H.1955. Fluctuations of animal populations and a measure of community stability. *Ecology* **36,** 533-536

MacArthur, R. H.1965. Patterns of species diversity. *Biological Reviews* 40**:**510-533 (1965).

MacArthur, R. H. and J. W. MacArthur, 1961. On bird species diversity. *Ecology* 42:594-98

MacArthur, R. H. and E. O. Wilson, 1967. *The Theory of Island Biogeography*, Princeton University Press, Princeton, New Jersey, USA

Mackey, R. L. & Currie, D. J. 2001. The diversity-disturbance relationship: is it generally strong and peaked? *Ecology* 82:3479-3492.

Margalef, R. 1967. Laboratory analogues of estuarine plankton systems. pp. 515–524. In: *Estuaries*. G. H. Lauff (ed.). American Association for the Advancement of Science, Washington, DC.

Margalef, R. 1968. *Perspectives in Ecological Theory*. University of Chicago Press, Chicago, IL.

Margalef, R. 1969. Diversity and stability: A practical proposal and a model of interdependence. pp. 25–37. In: *Diversity and Stability in Ecological Systems*. BNL-50175, Brookhaven National Laboratory, Upton, NY.

Margalef, R. 1984. Simple facts about life and the environment not to forget in preparing schoolbooks for our grandchildren. pp. 299–320. In: *Trends in Ecological Research for the 1980s*. J. H. Cooley and F. B. Golley (eds.). Plenum Press, New York.

Margalef, R. 1985. From hydrodynamic processes to structure (information) and from information to process. pp. 200–220. In: *Ecosystem Theory for Biological Oceanography*. R. E. Ulanowicz and T. Platt (eds.). Canadian Bulletin of Fisheries and Aquatic Sciences 213, Department of Fisheries and Oceans, Ottawa, Canada.

May, R. M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.

McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* 191:92-94

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259-94

Mitsch, W. J. 1991. Ecological engineering: approaches to sustainability and biodiversity in the U.S. and China. pp. 428–448. In: *Ecological Economics: The Science and Management of Sustainability*. R. Costanza (ed.). Columbia University Press, New York.

Mitsch, W. J. 1992. Wetlands, ecological engineering, and self-design. *Great Lakes Wetlands Newsletter.* 3:1–3,7.

Mitsch, W. J. 1993. Ecological engineering — a cooperative role with the planetary life support systems. *Environmental Science and Technology.* 27:438–445.

Mitsch, W. J. 1994. Ecological engineering: a friend. *Ecological Engineering.* 3:112–115.

Mitsch, W. J. 1995a. Ecological engineering: from Gainesville to Beijing — a comparison of approaches in the United States and China. pp. 109–122. In: *Maximum Power: The Ideas and Applications of H. T. Odum*. C. A. S. Hall (ed.). University Press of Colorado, Niwott, CO.

Mitsch, W. J. 1995b. Restoration and creation of wetlands — providing the science and engineering basis and measuring success. *Ecological Engineering.* 4:61–64

Mitsch, W. J. 2012. What is ecological engineering. *Ecological Engineering* 45:5-12

Mitsch, W. J. and S. E. Jorgensen. 2003. Ecological engineering: A field whose time has come. *Ecological Engineering* 20: 363-377

Mulder, C. P. H., Uliassi, D. D. *et al*. 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. *Proceedings of the National Academy of Sciences, USA* 98**:**6704-6708

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

Odum, E. P., 1969. The strategy of ecosystem development. *Science* 164:262-70

Odum, E. P. 1971. Fundamentals of Ecology. W. B. Saunders, Philadelphia, Pennsylvania

Odum, E. P. 1972. Ecosystem theory in relation to man. pp. 11–24. In: *Ecosystem Structure and Function*. J. A. Wiens (ed.). Oregon State University Press, Corvallis, OR.

Odum, E. P. 1984. The mesocosm. *BioScience.* 34:558–562.

Odum, E. P. and A. A. de la Cruz. 1963. Detritus as a major component of ecosystems. *AIBS Bulletin (BioScience).* 13:39–40.

Odum, E. P., E. H. Franz, and J. T. Finn. 1979. Perturbation theory and the subsidy-stress gradient. *BioScience* 29:349–352.

Odum, H. T. 1960. Ecological potential and analogue circuits for the ecosystem. *American Scientist.* 48:1–8.

Odum, H. T. 1967. Biological circuits and the marine systems of Texas. pp. 99–157. In: *Pollution and Marine Ecology*. T. A. Olson and F. J. Burgess (eds.). John Wiley & Sons, New York.

Odum, H. T. 1971. *Environment, Power, and Society*. John Wiley & Sons, New York.

Odum, H. T. 1972. An energy circuit language for ecological and social systems: its

Odum, H. T. 1983. *Systems Ecology: An Introduction*. John Wiley & Sons, New York.

Odum, H. T. 1985. Self-Organization of Ecosystems in Marine Ponds Receiving Treated Sewage. UNC Sea Grant Publication UNC-SG-85-04, North Carolina State University, Raleigh.

Odum, H. T. 1989a. Ecological engineering and self-organization. pp. 79–101. In: *Ecological Engineering*. W. J. Mitsch and S. E. Jørgensen (eds.). John Wiley & Sons, New York.

Odum, H. T. 1989b. Experimental study of self-organization in estuarine ponds. pp. 291–340. In: *Ecological Engineering*. W. J. Mitsch and S. E. Jørgensen (eds.). John Wiley & Sons, New York.

Odum, H. T. 1994a. Ecological engineering: the necessary use of ecological self-design. *Ecological Engineering.* 3:115–118.

Odum, H. T. 1994b "Emergy" evaluation of biodiversity for ecological engineering. pp. 339–359. In: *Biodiversity and Landscapes*. K. C. Kim and R. D. Weaver (eds.). Cambridge University Press, New York.

Odum, H. T. 1995. Self-organization and maximum empower. pp. 311–330. In: *Maximum Power: The Ideas and Applications of H. T. Odum*. C. A. S. Hall (ed.). University Press of Colorado, Niwot, CO.

Odum, H. T. 1996. *Environmental Accounting, Emergy and Environmental Decision Making*. John Wiley & Sons, New York.

Odum, H. T. 1996. Scales of ecological engineering. *Ecological Engineering*. 6:7–19.

Odum, H.T. and C.M. Hoskins. 1957. Metabolism of a laboratory stream microcosm. *Publ. Inst. Mar. Sci. Univ. Texas.* 4:115-133

Pace, M. L. *et al*. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14:483-488).

Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65-75

Paine, R. T. 1969. A note trophic complexity and community stability. *American Naturalist* 103:91-93

Paine, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* 52:1096-1106

Paine, R. T. 1976. Size-limited predation: and observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57:858-73

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49: 667-85

Petraitis, P. S., Latham, R. E. *et al*. 1989. The maintenance of species diversity by disturbance. *The Quarterly Review of Biology* 64**:**393-418

Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321-326.

Power, M. E. 1990. Effects of fish on river food webs. *Science* 250:811-14

Power, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* **73,** 1675-88.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L.S. Mills, G. Daily, J. C. Castilla, J. Lubchenko, and R. T. Paine 1996. Challenges in the quest for keystone species. *BioScience* 46:609-20

Preston, F. W. 1948. The commonness and rarity of species. *Ecology* 29:254-83

Reich P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Science* USA. 94: 13730-13734

Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions* 8**:**927-39.

Rosenzweig, M. L. 1968. Net primary productivity of terrestrial environments: predictions from climatological data. *American Naturalist* 102:67-84

Rosenzweig, M. L. 1992. Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy* 73:715-30

Sakamoto, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. *Arch. Hydrobiol*. 62: 1-28

Sala, O. E., W. J. Parton, L. A. Joyce, and W.K. Laurenroth. 1988. Primary production of the central grassland regions of the United States. *Ecology* 69:40-45

Schindler, D. E., Hilborn, R., *et al*. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465: 609-13

Schmid, B. 2002. The species richness-productivity controversy. *Trends In Ecology & Evolution* 17**:**113-14

Shaver, G. R. and F. S. Chapin III. 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, U. S. A. *Arctic and Alpine Research* 18:261-68

Simberloff, D. and W. Boecklen. 1981. Santa Rosalia reconsidered: size ratios and competition. Evolution: 35: 1206-1228.

Smith, S. D., Huxman, T. E. Zitzer, S. F., Charlet, T. N., Housman, D. C., Coleman, J.S., Fenstermaker L. K., Seemann, J. R., and Nowak, R. S. 2000. Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature* 408: 79-82

Smith, R.L. and T.M. Smith. 2001. Ecology and field biology, 6th ed. Benjamin Cummings, San Francisco.

Sousa, W. P. 1979a. Distubance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60**:**1225-1239.

Sousa, W. P. 1979b. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227-54

Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-91

Sousa, W. P. 2001. "Natural disturbance and the dynamics of marine benthic communities," in *Marine Community Ecology*, eds. M. D. Bertness, S. D. Gaines, *et al*. (Sunderland, MA: Sinauer Associates, 2001): 85-130.

Stachowicz, J. J., Bruno, J. F., *et al*. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology, Evolution and Systematics* 38**:**739-66

Stachowicz, J. J. & Byrnes, J. E. 2006. Species diversity, invasion success and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Marine Ecology Progress Series* 311:251-62

Straskraba, M. 1993. Ecotechnology as a new means for environmental management. *Ecological Engineering.* 2:311-331

Straskraba, M. 1993. Some new data on latitudinal differences in the physical limnology of lakes and reservoirs. In: Boltovskoy, A. and Lopez, H. L. (eds.). Functioning of Freshwater Ecosystems, Cambridge University Press. Cambridge, pp. 13-84

Straskraba, M. and Gnauck, H. 1985. Freshwater Ecosystems: Modelling and Simulation. Elsevier, Amsterdam.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73**:**747-54

Sukachev, V. N. 1944. On the principles of genetic classification in biocoenology. *Zurnal Oscei Biologii.* 5(4): 213-227

Summerson, H. C. & Peterson, C. H. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Marine Ecology Progress Series* 15:63-77

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284-307

Teal, J. M. 1991. Contributions of marshes and saltmarshes to ecological engineering. Pp 55-62 In: Ecological Engineering for Wastewater Treatment. C. Etnier and B. Guterstam (eds.). Bokskogen, Gothenburg, Sweden

Terborgh, J. *et al*. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923-1926.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach*. Ecology* 58:338-48

Tilman, D. 1982. Resource competition and community structure. *Monogr. Pop. Biol*. 17. Princeton University Press, Princeton, N. J.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2-16

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350-63.

Tilman, D. & Downing, J. A. 1994. Biodiversity and stability in grasslands. *Nature* 367**:**363-65

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277(5330): 1300-1302

Uhlman, D. 1983. Entwicklungstendenzen der Okotechnologie. Wiss. Z. Tech. Univ. Dresden 32. 109-116

Waide, J. B. and J. R. Webster, 1976. Engineering systems analysis: applicability to ecosystems. Pages 329-371 In: B. C. Patten (ed.) System analysis and simulation in ecology. Academic press. New York, USA.

Werner, E. E. and G. G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. *American Zoologist* 21:813-29

Willis, A. J. 1997. The ecosystem as an evolving concept. *Functional ecology* 11: 268-271

Worm, B., Barbier, E. B., *et al*. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787-90

Wootton, J. T.1992. Indirect effects, prey susceptibility, and habitat selection: Impacts of birds on limpets and algae. *Ecology* **73,** 981-91.

Yachi, S. & Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences, USA* 96:1463-68

Glossary

abiotic	An environmental effect or condition that is not directly caused or induced by organisms.
abiotic interactions	Interactions between living organisms and their physical environment
abiotic condensation	Nonenzymatic reaction of quinones with other organic materials in soil
abundance	The total number of individuals, or biomass, of a species present in a specified area
absolute humidity	Fraction of the global solar irradiance incident on a surface that is absorbed
absorbed photosynthetically active radiation	. Visible light (400 to 700 nm) absorbed by plants.
acclimation	Proximate physiological changes by an organism to artificially induced environmental conditions that enable it to withstand those conditions
acclimatization	Proximate physiological changes by an organism to conditions in the natural environment that enable it to withstand those conditions
acid rain.	Rain that has low pH, due to high concentrations of sulfuric and nitric acid released from combustion of fossil fuels.
actual evapotranspiration	Annual evapotranspiration at a site; a climate index that inte- grates temperature and moisture availability
adaptation	The process and structures by which organisms adjust to changes in their environment
age class	Individuals in a population of a particular age
age structure	The relative numbers of individuals in each age class
A horizon	Uppermost mineral zone of soil
allelochemicals	A substance produced by one organism that affects the growth and behavior of another species

allelopathy	The negative chemical influence of plants on one another
Allen's rule	According to this hypothesis, vertebrates living in cold environments tend to have shorter appendages than those living in warmer environments
allochthonous input.	Input of energy and nutrients from outside the ecosystem; synonymous with subsidy.
allometric relationship.	Regression relationship that describes the biomass of some part of an organism as a function of some easily measured parameter (e.g., plant biomass as a function of stem diameter and height).
allopatric	Occurring in different geographic areas. Used to describe the situation in which populations or species have nonoverlapping geographic ranges
altruism	Helping behavior in which one organism enhances the fitness of another at the risk of reducing its own evolutionary fitness
amensalism	A biotic interaction in which the activities of one partner species has a large effect on the other with the other species having little or no effect on the first
ammonification	Conversion of organic nitrogen to ammonium due to the breakdown of litter and soil organic matter; synonymous with *nitrogen mineralization*
anaerobic	Occurring in the absence of oxygen.
annual	An organism, usually a plant, that completes its life cycle from birth to reproduction to death in a year
anoxic	Aquatic or soil environment with low dissolved oxygen and unable to support most life
anthropocene	Geologic epoch characterized by human impacts, initiated with the Industrial Revolution.
anthropogenic	Resulting from or caused by people.
assimilation	The process by which inorganic substances are incorporated into organic molecules
assimilation efficiency	The percentage of energy ingested in food that is assimilated into the protoplasm of an organism
Assimilatory	Conversion of nitrate to amino acids by soil microbes.

nitrate reduction.

atmosphere	The gaseous envelope surrounding the earth
autecology	The study of an individual organism or a single species of organism and its environment
Autochthonous production	Production occurring within the ecosystem.
autotroph	Organism that produces organic matter from CO_2 and environmental energy rather than by consuming organic matter produced by other organisms. Most produce organic matter by photosynthesis; synonymous with *primary producer*
B horizon	Soil horizon with maximum accumulation of iron and aluminum oxides and clays.
behavior	The observable response of organisms to stimuli
behavioral ecology	The study of the role of an organism's behavior in determining its ecology
benthic	Refers to the bottom or sediment habitats in aquatic environments
benthos	Organisms that dwell in sediments or the bottom of aquatic habitats
Bergmann's rule	The hypothesis that homeotherms that live in colder climates tend to have larger body size than those in warm climates. This enables them to conserve heat more efficiently because of their surface area to volume ratio
biogenic	Biologically produced
biogeochemical cycling	Biologically mediated cycling of materials in ecosystems
biomass	Quantity of living material (e.g., plant biomass).
biosphere	Biotic component of Earth, including all ecosystems and living organisms.
biotic	Caused or induced by organisms
Biochemical Oxygen Demand (BOD)	The amount of oxygen that would be consumed if all the organic substances in a given volume of water were oxidized by bacteria and other organisms; reported in milligrams per liter

biodiversity	Another name for biological diversity. there three main categories of biodiversity namely: genetic diversity, species diversity and habitat or ecological diversity
biogeochemical cycle	The cycling of elements between atmospheric, geological and biological pools in the biosphere
biogeography	The study of the geographical distribution of organisms
biomagnification	The increasing concentration of a substance in tissues of consumers as it passes through lower to higher trophic levels
biomass	The dry weight of living material in all or part of an organism, population or community
biome	Global-level category of ecological regions determined primarily by climatic conditions
bioremediation	The use of living organisms to remove ecologically harmful substances from the environment
biosphere	The part of earth atmosphere in which life exist
biotic interactions	Interactions between living organisms
biotic resistance hypothesis	The idea that species-rich communities are more resistant to invasion than species-poor communities
bottom-up controls	Regulation of consumer populations by quantity and quality of food.
bulk density	Mass of soil per unit volume
C horizon	Soil horizon that is relatively unaffected by the soil forming processes
carbon-based defense.	Organic compounds that contain no nitrogen and defend plants against pathogens and herbivores.
carbon-nitrogen balance hypothesis	The idea that the allocation of carbon and nitrogen to plant defenses are dependent on their availability in the environment
carnivore	An animal or plant that eats animals
carrying capacity	The maximum population size of a species that the resources of a habitat or ecosystem can support

character displacement	Divergence in the characteristics of two otherwise similar species where their ranges overlap, caused by competition between the species in the area of overlap
chemical alteration	The first phase of decomposition where fungi and bacteria chemically change dead organic matter
chronosequence	The change in community structure primarily influenced by time such that older communities appear different to younger communities
climate	The prevailing patterns of weather in a given area
climax community	The community capable of indefinite self-perpetuation under given climatic conditions
colonization hypothesis	The idea that seed dispersal is advantageous to plants because seed germination is not ideal in the vicinity of parent plants
commensalism	This is a feeding relationship between two different kinds of nonparasitic animals (commensals), that is harmless to both and in which one of the organism benefits
community	An assemblage of microbes, plants and animals living and interacting in a specified location. Communities are the biotic component of ecosystems
community ecology	The branch of ecology concerned with the study of the interactions between species in ecosystems and how these interactions affect ecosystem processes
competition	The interaction that occurs when organisms of the same or different species use a resource that is limited in supply.
competitive avoidance hypothesis	The idea that seed dispersal is advantageous to plants because competition between parent plants and seedlings is avoided.
competitive exclusion principle	The hypothesis that two or more species cannot occupy the same niche i.e. occupy the same physical location and use the same resources in that location
connectance	The number of actual links in a food web divided by the number of potential links in the same food web
connectedness webs	Food webs detailing all the known possible feeding relationships of organisms within the community
connectivity.	Degree of connectedness among patches in a landscape.

conspecific	Belonging to the same species
consumption efficiency	The percentage of energy at one trophic level that is consumed by the next higher trophic level
consumers	These are the animals that depend directly or indirectly on plants
coriolis force	The effect of the Earth's rotation on the surface flow of winds
deciduous	Shedding leaves in response to specific environmental cues.
decomposers	Consumers that get their energy and nutrients from the dead bodies, parts or waste products of other organisms
decomposition	The physical and chemical breakdown of detritus
density-dependent factor	Biotic factors in the environment, such as disease and competition which can be directly influenced by the density of organisms in the habitat they occupy
density-independent factor	Abiotic conditions such temperature which are not directly influenced by the density of organisms in the habitat they occupy
denitrification	Enzymatic reduction by bacteria of nitrates to nitrogen gas
detritivores	Non-microbial organisms that eat detritus and facilitate its decomposition by microorganisms
detritivory	The consumption of detritus that is carried out mostly by invertebrate organisms such as earthworms, termites, and ants. Detritivory facilitates the decomposition process carried out mainly by bacteria and fungi
detritus	Dead plant and animal material and animal waste products
disturbance	An event, relatively discrete in time and space, that alters the structure of a community or ecosystem.
disturbance regime	The range of severity, frequency, type, size, timing, and intensity of disturbances characteristic of an ecosystem or region.
disturbance severity	Magnitude of change in resource supply or environment caused by a disturbance.
diversity index	An index that measures the relative number of species in an area and the distribution of individuals among them

diversity-stability hypothesis	The idea that species-rich communities are more likely to be stable than species-poor ones
deposition	Atmospheric input of materials to an ecosystem.
dominant species	A Species that has a high effect in a community because of its dominance in numbers or biomass
E horizon	Heavily leached horizon beneath the A horizon; formed in humid climates.
ecology	The scientific study of the processes influencing the distribution and abundance of organisms, the interactions among organisms, and the interactions between organisms and the transformation and flux of energy and matter
ecosystem	Ecological system consisting of all the organisms in an area and the physical environment with which they interact.
ecosystem ecology	Study of the interactions between organisms and their environment as an integrated system.
ecosystem engineer	Organisms that alter resource availability by modifying the physical properties of soils and litter.
ecosystem processes	Inputs or losses of materials and energy to and from the ecosystem and the transfers of these substances among components of the system.
ecotone	A spatial transition from one type of ecosystem to another.
ectotherm	An organism that relies mainly on external sources of energy for regulating body temperature
ectoparasite	They are parasites that live on the surface of the host and derived their food
endoparasite	They are parasites that live inside the body of the host
entropy	The process whereby energy loses its capacity to do work
environment	Everything associated with organisms, including living and non-living part of the world
euphotic zone	Uppermost layer of water in aquatic ecosystems where there is enough light to support photosynthesis.
eutrophic	Nutrient rich
eutrophication	Nutrient-induced increase in productivity.

evapotranspiration	Water loss from an ecosystem by transpiration and surface evaporation.
facilitation	Processes by which some species make the environment more favorable for the growth of other species.
field capacity	Water held by a soil after gravitational water has drained.
flux	Flow of energy or materials from one pool to another.
food chain	A linear feeding relationship involving transfer of energy through food, from producers to consumers
food web	A complex inter connecting feeding relationship among plants and animals in an ecosystem
functional type	Group of species defined by their similarity in how they affect (effects functional type) or respond to (response functional type) the environment and ecosystem processes
geographic information system	A computer-based system that stores, analyzes and displays geographic information, generally in the form of maps
geometric population growth	Population growth in which populations do not overlap and in which successive generations differ in population size by a constant ratio
greenhouse effect	Warming of the earth's atmosphere and surface as a result of heat trapped near the earth's surface by gases in the atmosphere, especially water vapor, carbon dioxide, methane, ozone, nitrous oxide and chloroflourocarbons
generalist herbivore	Herbivore that is relatively nonselective in its choice of plant species.
grazer	Herbivore that consumes herbaceous plants (terrestrial ecosystems) or periphyton (aquatic ecosystems).
grazing lawn	Productive grassland or wetland ecosystem in which plants are heavily grazed but supported by large nutrient inputs from grazers.
gross primary production	The total amount of energy fixed by all the autotrophs in an ecosystem
groundwater	Water in soil and rocks beneath the rooting zone.

growth	Production of new biomass.
guild	A group of organisms that make their living in a similar way. For example, frugivorous bats, insectivorous birds, herbivorous mites etc.
hadal zone	The deepest parts of the oceans, below about 6,000 meters
habitat	The natural dwelling place of an organism
herbivore	A heterotrophic organism that eats plants
heterotroph	An organism that uses organic molecules both as source of energy and source of carbon
hibernation	A dormant state by animals during with metabolic rate is reduced. Usually occurs during periods of harsh conditions such as winter or drought
homeotherm	An organism that uses metabolic energy to maintain a relatively constant body temperature
horizon	Layer in a soil profile. The horizons, from top to bottom, are the O horizon, which consists of organic matter above mineral soil; the A horizon, a dark layer with substantial organic matter; the E horizon, which is heavily leached; a B horizon, where iron and aluminum oxides and clays accumulate; and a C horizon, which is relatively unaffected by soil-forming processes.
hot spot	Zone of high rates of biogeochemical processes in a soil or landscape.
humus	Amorphous soil organic matter that is the final product of decomposition.
hydrologic cycle	The cycle of water through the biosphere which is driven by solar energy and involves the processes of evaporation, transpiration, condensation, precipitation and runoff
hydrosphere	The water portion of the earth’s crust comprising the ocean, sea, and all their waters
hyperosmotic	A term that describes organisms with body fluids which have a lower concentration of water and higher solute concentration than the external environment
igneous rocks	Rocks formed when magma from Earth's core cools near the surface.
immobilization	Removal of inorganic nutrients from the available pool by microbial uptake and chemical fixation.

infiltration	Movement of water into the soil.
interactive controls	Factors that control and respond to ecosystem characteristics, including resource supply, modulators, major functional types of organisms, disturbance regime, and human activities.
inhibition model	A model of succession that proposes that early occupants of an area modify the environment in a way that makes the area less suitable for both early and late successional species
insectivore	A heterotrophic organism that eats insects
interference competition	A form of competition that involves aggressive interactions between individuals
interspecific competition	Competition between individuals of different species
intraspecific competition	Competition between individuals of the same species
idiosyncratic hypothesis	The idea that community function and species richness are not linked in a predictable way
immigration	The movement of individuals into a population
inbreeding	A mating system in which adults mate with relatives more often than would be expected by chance
inclusive fitness	The total genetic contribution of an individual to future generations through its offspring and relatives
indicator species	Species whose status provides information on the overall health of an ecosystem
indirect effect	An effect of one species on another that is mediated by a third species
individualistic model	The view that a biotic community is an assemblage of species coexisting primarily because of similarities in their physiological requirements and tolerances
induced defenses	Plant defenses that are only switched on following herbivore attack
insurance hypothesis	The idea that a surplus of species exists in communities as a way of reducing the adverse effects of the loss of a species in the community.

intermediate disturbance hypothesis	The idea that ecosystems subjected to intermediate levels of disturbance tend to have higher primary productivity and higher species diversity than those that have not
intermediate host	One or more of species of host in which macroparasites develop but do not undergo sexual reproduction
introduced species	A species living outside its native range; also known as exotic, alien, nonnative or nonindeginous
invasional meltdown	The idea that the invasion of a community by exotic species predisposes the community to further invasion by more exotic species
invasive species	Introduced species that are spreading in their new range and often cause harm to native species
k-selected species	Species that have a relatively low rate of per capita rate of population growth, r, but that exists near the carrying capacity, K, of the environment.
keystone hypothesis	The idea that most species are vital to the functioning of ecosystems and that function decreases immediately as species richness declines
keystone species	A species having a disproportionately large impact on the ecosystem despite having a relatively low biomass contribution to the community
lithosphere	This is earth outer layer of varying thickness lying with a mass of rock several kilometers thick
Liebig's Law of the minimum.	Plant growth is limited by a single resource at any one time; another resource becomes limiting only when the supply of the first resource is increased above the point of limitation.
litter	Dead plant material that is sufficiently intact to be recognizable.
littoral zone	Shore of a lake or ocean.
macrofauna	Soil animals larger than 10 mm in length.
macronutrients	Nutrients that are required in large quantities by organisms.
mass flow	Bulk transport of solutes due to the movement of soil solution.
mesofauna	Soil animals 0.2 to 10 mm in length.
metamorphic rocks	Sedimentary or igneous rocks that are modified by exposure to heat or pressure.

metapopulation	A group of subpopulations living in separate locations with active exchange of individuals among subpopulations
microbial loop	Microbial food web (including both plant- and detritus-based organic material) that recycles carbon and nutrients within the euphotic zone.
microbial transformation	Transformation of plant-derived substrates into microbial- derived substrates as a result of microbial turnover.
microbivore	Organism that eats microbes
microfauna	Soil animals less than 0.2 mm in length.
micronutrients	Nutrients that are required in small quantities by organisms
mineralization	Conversion of carbon and nutrients from organic to inorganic forms due to the breakdown of litter and soil organic matter. Gross mineralization is the total amount of nutrients released via mineralization (regardless of whether it is subsequently immobilized or not). Net mineralization is the *net* accumulation of inorganic nutrients in the soil solution over a given time interval.
modulator	Factor that influences growth rate but is not consumed in the growth process (e.g., temperature, ozone).
mutualism	Symbiotic relationship in which there is the mutual relationship between two organisms in which both (symbionts) benefits
mycorrhizae	Symbiotic relationship between plant roots and fungal hyphae, in which the plant acquires nutrients from the fungus in return for carbohydrates that constitute the major carbon source for the fungus.
mycorrhizosphere	Zone of soil that is directly influenced by mycorrhizal hyphae.
negative feedback	Interaction in which two components of a system have opposite effects on one another; this reduces the rate of change in the system.
net primary production	The amount of energy left after autotrophs have met their own energetic needs. This is calculated as gross primary production minus respiration by primary producers. It is the amount of energy that is available to consumers in an ecosystem

niche	Ecological role of an organism in an ecosystem
nitrification	Conversion of ammonium to nitrate in the soil. Autotrophic nitrifiers use the energy yield from NH_4+ oxidation to fix carbon used in growth and maintenance, analogous to the way plants use solar energy to fix carbon via photosynthesis. Heterotrophic nitrifiers gain their energy from breakdown of organic matter.
nitrogenase	Enzyme that converts dinitrogen to ammonium
nitrogen-based defense	Plant defensive compound containing nitrogen
nitrogen fixation	Conversion of dinitrogen gas to ammonium
nutrient	A chemical substance required for the development, maintenance and reproduction of organisms
nutrient cycling	Mineralization and uptake of nutrients within an ecosystem patch
nutrient uptake	Nutrient absorption by plant roots.
nutrient retentiveness	The tendency of an ecosystem to retain nutrients
nature	Every living and non-living things in the universe
niche	The functional role an organism plays in the community
o horizon	Organic horizon above mineral soil.
oligotrophic	Nutrient poor.
omnivore	Organism that eats food from several trophic levels.
oxidation	Loss of electrons by an electron donor in oxidation-reduction reactions
parent material	Rocks or other substrates that conditions of light, moisture, and generate soils through weathering
patch	Relatively homogeneous stand of an ecosystem in a landscape
pelagic	Open water
periphyton	Algae that attach to rocks, vascular plants, and any other stable surfaces
permanent wilting	Water held by a soil that cannot be extracted by plant uptake

point	
perturbation	An external force that displaces a system from equilibrium
phenology	Time course of periodic events in organisms that are correlated with climate
photoperiod	Daylength
photosynthesis	Biochemical process that uses light energy to convert CO_2 to sugars. Net photosynthesis is the net carbon input to ecosystems; synonymous at the ecosystem level with gross primary production.
photosynthetically active radiation	Visible light; radiation with wavelengths between 400 and 700 nm.
phototroph	Nitrogen-fixing microorganism that produces its own organic carbon through photosynthesis
phreatophyte	Deep-rooted plant that taps groundwater.
phyllosphere decomposition	Decomposition that occurs on leaves before leaf fall.
phytoplankton	Microscopic algae suspended in the surface water of aquatic ecosystems
plankton	Microscopic organisms suspended in the surface water of aquatic ecosystems
pioneer community	The first community, in a successional sequence of communities, to be established following a disturbance
plant-based trophic system	Plants, herbivores, and organisms that consume herbivores and their predators.
plant defense	Chemical or physical property of plants that deters herbivores
precipitation	Water input to an ecosystem as rain and snow.
primary producers	Organisms that convert CO_2, water, and solar energy into biomass (i.e., plants); synonymous with *autotroph*

primary production	Conversion of CO_2, water, and solar energy into biomass. Gross primary production is the net carbon input to ecosystems, or the net photosynthesis expressed at the ecosystem scale (g C m^2 yr^1). Net primary production is the net carbon accumulation by vegetation (GPP minus plant respiration
primary succession	Succession following severe disturbances that remove or bury most products of ecosystem processes, leaving little or no organic matter or organisms
potential biota	Organisms that are present in a region and could potentially occupy the site
production efficiency	Proportion of assimilated energy that is converted to animal production, including both growth and reproduction
R horizon	Unweathered bedrock at the base of a soil profile also known as the regolith
regolith	Unweathered bedrock layer.
relative accumulation rate	Nutrient uptake per unit plant nutrient
resilience	The capacity to recover community structure and function after a disturbance. Measured as the rate at with which a system returns to its reference state after a perturbation.
resource limitation	The limitation of population growth by resource availability
rhizosphere	Zone of soil that is directly influenced by roots
rock cycle	Formation, transformation, and weathering of rocks
runoff	Water loss from an ecosystem in streams and rivers
resource	Substance that is taken up from the environment and consumed in growth (e.g., light, CO_2, water, nutrients).
sand	Soil particles 0.05 to 2 mm diameter
saturated flow	Drainage of water under the influence of gravity.
savanna	Grassland with scattered trees or shrubs.
secondary producers	Herbivores and carnivores
secondary succession	Succession that occurs on previously vegetated sites after a disturbance in which there are residual effects of organisms and organic matter from organisms present before the disturbance

secondary consumers	These are the flesh eating animals
sedimentary rocks	Rocks formed from sediments.
shredder	Invertebrate that breaks leaves and other detritus into pieces and digests the microbial jam on the surface of these particles.
soil organic matter	Dead organic matter in the soil that has decomposed to the point that its original identity is uncertain
species composition	Identity of species in an ecosystem.
species diversity	Number, evenness, and composition of species in an ecosystem; the total range of biological attributes of all species present in an ecosystem
species evenness	Relative abundances of species in an ecosystem.
species richness	Number of species in an ecosystem.
state factors	Independent variables that control the characteristics of soils and ecosystems (climate, parent material, topography, potential biota, and time).
succession	Directional change in ecosystem structure and functioning resulting from biotically driven changes in resource supply
symbiosis	Interdependence of different species
symbionts	Each of the species of organisms that live together
sympatric	Occurring in the same place
tertiary consumers	Organisms that eat secondary consumers
thermosphere	Outermost layer of the atmosphere, which is characterized by an increase in temperature with height.
theory of island biogeography	This theory states that the number of species on an island tends toward an equilibrium number that is determined
tilt	Angle of Earth's axis of rotation and the plane of its orbit around the sun
top-down controls	Regulation of population dynamics by predation
trophic cascade	Top-down effect of predators on the biomass of organisms at lower trophic levels; results in alternation of high and low biomass of organisms in successive trophic levels.

trophic dynamics	The transfer of energy from one part of an ecosystem to another
trophic efficiency	Proportion of production of prey that is converted to production of consumers at the next trophic level.
trophic interactions	Feeding relationships among organisms.
trophic level	Organisms that obtain their energy with the same number of steps removed from plants or detritus.
troposphere	Lowest layer of the atmosphere, which is continually mixed by weather systems and is characterized by a decrease in temperature with height.
upwelling	Upward movement of deep and intermediate ocean water, usually driven by offshore winds near coasts
vapor pressure deficit	The difference between actual water vapor pressure and the saturation water vapor pressure at a particular temperature
water potential	The capacity of water to do work, which is determined by its free energy content; Water flows from positions of positions of higher to lower free energy. Increasing solute concentration decreases water potential
water vapor pressure	The atmospheric pressure exerted by the water vapor in air; increases as the water vapor in air increases
	Difference in soil water content between field capacity and permanent wilting point.
weathering	Processes by which parent rocks and minerals are altered to more stable forms. Physical weathering breaks rocks into smaller fragments with greater surface area. Chemical weathering results from chemical reactions between rock minerals and the atmosphere or water.
xeric	Characterized by plants that are tolerant of dry conditions
zonation of species	Pattern of separation of species into distinctive vertical habitats or zones
zooplankton	Microscopic animals suspended in the surface water of aquatic ecosystems