# BCS 311: Land and Environments of the Circumpolar World I

## Module 5: Ecological Principles

Developed by
Stig Skreslet
Marine Ecology, Faculty of Biosciences and Aquaculture
University of Nordland
Bodø, Norway

Adapted by
Alec Aitken
Department of Geography and Planning
University of Saskatchewan
Saskatoon, Saskatchewan, Canada

## Overview

Humans require simple concepts that explain how our environment functions if we are to survive and build sustainable societies that fulfill our basic needs. An ecosystem is a concept constructed from empirical results obtained by scientific research. It simply represents a three-dimensional space that encloses non-living and living constituents that obey rules for the flow of energy through the ecosystem and cycling of chemical matter within it. Ecological theory and principles allow us to construct models that explain how populations of different species grow and cooperate in spaces smaller than the ecosystem. No ecosystem is completely closed and communicates with other ecosystems within the biosphere of our planet. However, concepts that are too open and do not contain the most influential of interacting populations will be unstable and cannot provide reliable predictions of future development. Therefore, it is important to apply ecological principles in meaningful ways. Computer technology has now made possible the construction of numerical models based upon ecological concepts. They are helpful in facilitating our attempts to understand complex ecological processes. Some models already support appropriate ecosystem-based management of human interaction with ecosystems.

## Learning Objectives

Upon completion of this module, you should be able to:

1. Illustrate the hierarchy of biological systems.
2. Define common ecological concepts and how they apply to the North.

3. Discuss interrelations between biotic and abiotic elements of structural components.
4. Identify the major factors that regulate the size and dynamics of populations.
5. Examine varieties of interactions among organisms that contribute to the species composition of biotopes.
6. Identify the major factors that regulate ecosystem dynamics.

## Required Readings (including web sites)

CAFF. Arctic Flora and Fauna, Status and Conservation. 2001. Chapter 2. Ecology. Edita, Helsinki, pp.17-49. http://arcticportal.org/arctic-council/working-groups/caff-document-library/arctic-flora-and-fauna/

## Key Terms and Concepts

- Biome
- Carrying Capacity
- Community
- Ecosystem
- Food Web
- Migration
- Population
- Resiliency
- Resistance

## Learning Material

### Introduction

Ecology was established as a new field of science by Eugen Warming (1841-1924), a Danish botanist, who in 1895 argued that the world's geographical distribution of plant communities could be explained as a function of physical factors and interaction with animal communities. His ideas spread rapidly among biologists from Atlantic Europe to Russia and North America establishing ecology as a global science. However, to some extent, the vocabulary of new scientific terms evolved separately due to geographical distance, cultural traditions and political reasons. Differences in the understanding of scientific terms may be confusing for even experienced biology students. Furthermore, ecological concepts and principles presented in this text must be equally valid in terrestrial, freshwater and marine systems. Ecological principles in this module are, as much as possible, explained in plain English. However, good scientific terms are precise expressions of complex processes and relationships and ecologists have succeeded in establishing many scientific terms that express a distinct and universal meaning. Terms presented in bold letters in this text are explained when they emerge for the first time.

## 5.1 The Hierarchy of Biological Systems

Two influential American ecologists, Eugene P. Odum (1913-2002) and his brother, Howard T. Odum (1924-2002), established that in principle ecology deals with systems of organisms that utilize energy taken from their environment. Biological units may be regarded as organized in a hierarchy of biological systems from gene systems to ecosystems. Each level interacts with matter (biochemical components) and energy to establish biological systems (Figure 5.1). Ecological theory is associated with the three higher levels of biological units, organisms, populations and communities. They exchange matter and energy with their external environment and differ from lower biological units that deal with transformation matter and energy inside an organism.

| Biological Unit | | Biological System |
|---|---|---|
| • Gene<br>• Cell<br>• Organ | Transformation of matter and energy within organisms | • Gene system<br>• Cell system<br>• Organ system |
| • Organism<br>• Population<br>• Community | Exchange of matter and energy with the environment | • Organismic system<br>• Population system<br>• Ecosystem |

Figure 5.1. Classical organization levels in biology according to E.P. Odum.

The matter in question includes numerous gases, liquids and solid substances that living organisms use to grow and multiply. The direct effects of energy on organisms can occur within the planet's **biosphere**, a thin layer inhabited by organisms where liquid water is present. Its thickness is limited to the troposphere (the lower 8 – 15 km of the atmosphere), the depths of the oceans (11 km maximum depth range), lakes and rivers, and the topsoil on land (see Modules 6 and 7). All organisms inhabiting the biosphere constitute an entity that is a common product of evolution. They may be subdivided into smaller spatial entities forming assemblages of different species present within a defined space that scientists refer to as **biota**. The biosphere is, of course, the largest of all biota.

## 5.2 The Ecosystem

### Definition

An ecosystem can be categorized into its **abiotic** constituents, including minerals, climate, soil, water, sunlight and all other nonliving elements and its **biotic** constituents, consisting of all its living members. Linking these constituents together are two major forces: the flow of energy through the ecosystem and the cycling of matter within the ecosystem (Encyclopædia Brittanica, 2009; Ricklefs, 1990).

## 5.3 The Structure of Ecosystems

### Structural Components

An ecosystem is a conceptual model established to explain how a functional unit of nature works. The model contains five structural components:

1. Inorganic Matter
2. Climate
3. Producers
4. Consumers
5. Decomposers

Items 1 and 2 represent abiotic components while items 3 to 5 represent biotic elements (Figure 5.2). Living organisms of an ecosystem are organized into **populations** of individuals that cooperate to reproduce genetic capacities that have proven successful in their environment. The sum of all populations is the ecosystem's **community** of organisms (Figure 5.1).

An ideal ecosystem should maintain all of its biotic components within a defined space, but no ecosystem is completely closed. To a certain extent they all exchange matter and energy with other ecosystems, but spaces that import many of their biotic elements from or export many of their biotic elements to other spaces do not qualify as real ecosystems.

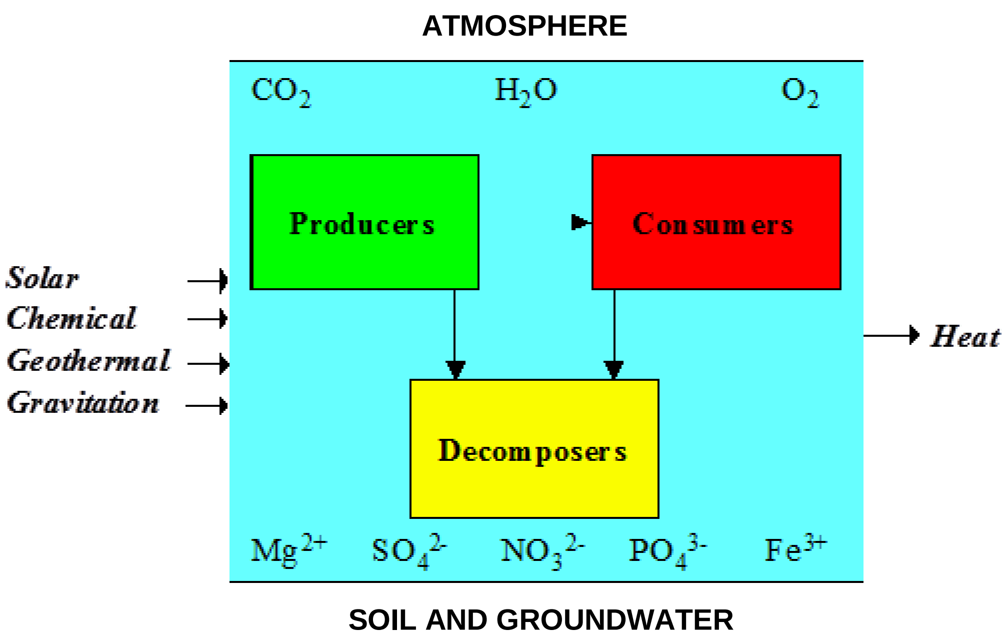


Figure 5.2. Simple presentation of a true ecosystem within a closed geographic space (main box), sources of inorganic matter (chemical symbols), organisms organized in functional groups (rectangles) and flows of energy (arrows).

## Abiotic Elements

All kinds of life form the biosphere of our planet. None can exist without water ($H_2O$). Its uptake in organisms and presence in their environment prevents them from being desiccated, but it is also an important element in the production and decomposition of **biomass**, the organic matter produced by living organisms (Figure 5.2). Gases such as oxygen ($O_2$) and carbon dioxide ($CO_2$) present in the atmosphere dissolve in water. Water also plays an active role in weathering rocks releasing mineral ions into solution. Ions like phosphate ($PO_4^{3-}$), nitrate ($NO_3^-$), sulphate ($SO_4^{2-}$) and iron ($Fe^{2+}$ and $Fe^{3+}$) are essential to all forms of life. Magnesium ($Mg^{2+}$) is of particular importance to producers that build pigments capable of absorbing solar energy. These chemicals and many others are cycled between organisms, their environment and solid mineral deposits (Figure 5.9).

In ecology climate is understood as the physical and chemical variables in the environment inhabited by organisms, such as temperature, salinity, the flow of air and water, and sunlight (see Modules 2 and 7). Some **electromagnetic radiation** emitted from the sun that lies within the spectrum of visible light (wavelengths of 0.400 – 0.710 micrometres) is **photosynthetically active radiation** (PAR). This solar energy facilitates plant growth (Figure 5.3) and vision in animals that have eyes. Ultraviolet radiation (UV) is emitted at shorter wavelengths (0.01 – 0.40 micrometres) and may be detrimental to organisms that cannot produce protective molecules (pigments) in their tissues or take shelter from it. Infrared radiation (IR) is emitted at longer wavelengths (0.7 – 1000 micrometres) and is experienced as heat radiating from fire or dark-coloured rocks warmed by sunlight (Figure 5.3).

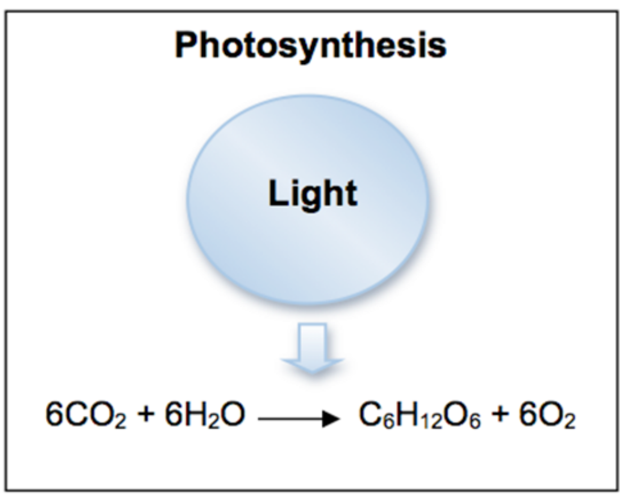


Figure 5.3a. Photosynthesis uses solar energy to produce an organic molecule (glucose) and oxygen ($O_2$) from water ($H_2O$) and carbon dioxide ($CO_2$). Plants extract carbon dioxide from the atmosphere through their leaves and water from the soil through their roots. Oxygen is released from plant leaves into the atmosphere.

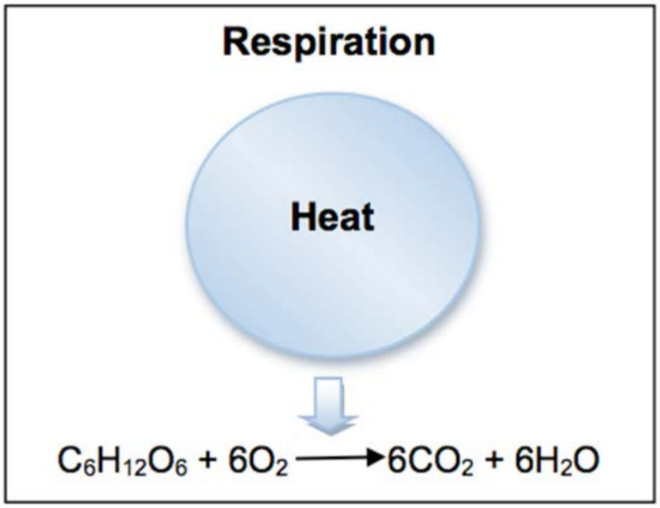


Figure 5.3b. Respiration reverses the process providing energy that is used in the synthesis of various plant tissues. Heat is the final output of energy from this ecological process. Oxygen from the atmosphere is consumed during respiration. Water vapour and carbon dioxide are released from plant leaves into the atmosphere.

Geochemical energy is exploited in many ecological processes. Some bacteria grow by using energy that binds atoms together in rocks or is contained in sulfuric molecules dissolved in water. **Geothermal energy** is heat conducted through the Earth's crust or released from magma moving through it (see Module 3). It may thaw ground in permafrost regions (see  Module 4) and is essential in hydrothermal communities of bacteria and animals associated with volcanic activity in the deep ocean.

Ecological processes obey the **Law of Conservation of Energy,** which states, "*Energy cannot be created or destroyed, only changed from one form to another"*. A biological system that receives a given amount of energy must release an equal amount of energy or store it as potential energy within organic matter. Ecosystems are very good at utilizing all available energy for the generation of biomass produced by their populations. All of the energy utilized by an ecosystem is ultimately released as **sensible heat** (Figure 5.3) and emitted as infrared radiation from Earth's surface (L↑) into the atmosphere or outer space (see Module 2).

## Biotic Elements

**Producers** of an ecosystem are also called **autotrophic** organisms, meaning they are "self-nourishing". They may be **phototrophic** organisms that assimilate solar energy or **chemotrophic** bacteria using energy stored as chemical bonds in inorganic molecules. The phototrophs are plants, algae and some specialized bacteria. Plants dominate on land and in shallow water in lakes. They are trees, grasses and herbs that have tubular vascular systems to transport water and its content of dissolved mineral nutrients acquired from the soil by their roots.  Algae dominate in the sea, but are also abundant in freshwater. They have no roots so their cells take up the dissolved minerals directly from the ambient water. Typical forms are kelps and seaweeds growing on the seafloor or phytoplankton that consists of single cells or chains of cells floating near the water surface.

Phototrophs utilize solar energy to split water and combine the released hydrogen atoms with carbon dioxide to form a carbohydrate molecule called glucose (Figure 5.3a). Oxygen is the byproduct of this process called **photosynthesis**. However, autotrophs also need to produce complex organic molecules other than glucose (e.g., proteins, fats). The energy required for their synthesis is taken from **respiration,** which the autotrophs perform by splitting stored glucose (Figure 5.3b). Carbon dioxide and water are returned to the environment and much of the energy that keeps complex molecules together is released as heat. The remaining energy is used to build new complex organic matter. Respiration operates day and night, mostly regulated by temperature, while photosynthesis operates only during daylight hours. Respiration relies on surplus energy in the form of sugars produced and stored in plant tissues during daytime to operate during the night.

Organisms that cannot survive on abiotic sources of chemicals and energy do so by digesting the biomass produced by other organisms. They obtain the energy for their growth and reproduction only from what they eat and release it for biochemical work when they decompose glucose and respire oxygen. They are termed **heterotrophs** meaning "other-feeders". They feed on the biomass originally produced by the **primary production** of autotrophs while their biomass is the result of **secondary production**.

Heterotrophs perform the role of **consumers** within an ecosystem. They pass their food through a system of digestive organs within their body. Those organisms that eat plants and algae are termed **herbivores.** However, because some consumers eat other producers than plants and algae, many ecologists prefer to use the synonyms **primary consumer** or **first order consumer**. Similarly, the term **carnivore**, which means "meat eater" may be substituted by **secondary consumer**. However, some carnivores hunt herbivores while some hunt other carnivores. That is why it is useful to apply the terms second, third and fourth (etc.) order consumers to describe who eats whom. The organism that is eaten is prey for its hunter, the predator. Man is an important consumer present in any conceivable ecosystem today. Humans exploit and feed on plants, algae and animals in many contexts and are classified as **omnivores,** animals that eat and digest nearly everything, much like the brown bear.

**Learning Activity 1**

**Consider a terrestrial or aquatic environment with which you are familiar. Try to identify common organisms in this environment and classify each organism into one of these categories: primary producer (autotroph); primary consumer (herbivore/omnivore); secondary consumer (carnivore/omnivore); tertiary consumer (carnivore/omnivore); detritivores/decomposers. Use arrows to indicate the flow of matter and energy among these various organisms.**

Another important group of consumers are **detritivores** that consume detritus, the organic remains of dead organisms or fecal matter from other animals. Some are non-selective and digest whatever is accumulated within soils and sediments or suspended in water. Detritivores recycle dead tissues by incorporating organic molecules and inorganic nutrients into their own living tissues, which are subsequently offered to their predators. However, they compete with **decomposers** such as heterotrophic fungi and bacteria. These organisms produce little biomass and release much energy as heat to the environment due to their respiration. The main role of an ecosystem's decomposers is to split organic molecules and release inorganic molecules, which recycle nutrients to active autotrophy. However, they do not consume with all of the biomass produced, which is evident in peat accumulated in swamps and fossilized deposits of coal, oil and gas stored in rocks (see Sedimentary Rocks in Module 3).

## 5.4 Population Dynamics

The biotic components of an ecosystem are the many different biological **species** that interact with their environment and each other. There is growing evidence that the environment selects for particular genetic capacities within a species and even within the progeny from the same mother. Some individuals may tolerate what some of their siblings do not. This is how biological evolution works. The process never stops and selects organisms with genetic properties compatible with ecological challenges in their environment. Organisms that cannot cope die without reproducing their genetic codes.

A species may form a number of separate **populations** in genetic terms. A population is a group of individual organisms that interbreed, meaning they exchange genes when they reproduce and transfer their biological properties to new generations. This group of organisms does not interbreed with other populations either because of biological differences or environmental barriers. Therefore, their population system exists within a geographical space. They interact with other species to form a biota that characterizes their population system.

Scientists and managers frequently subdivide animal populations into **stocks** to identify particular groups within a population. For example, a wintering stock of moose may congregate in a particular valley, while the spawning stock of a fish are adults coming together to reproduce in the spawning season. **Standing stock** is a numerical variable that describes the average number of animals per unit of area at a particular time. The similar terms for autotrophs are **crop** and **standing crop**.

Evolution improves the adaptation of species to their environment by selection according to two opposite strategies. One strategy results in species that are **r-strategists**, as expressed in the simple equation: $r = b - d$

Where r = rate of population growth

b = birth rate in a population

d = death rate in a population.

**K-strategists** represent the other strategy, as expressed in the equation:

$$I = r\frac{(K-N)}{K}N$$

This equation states that the increase or decrease in the number of individuals in a population during a period of time (I) is a function of r. The stability of the population size depends on the balance between the existing number of individuals (N) and the environment's **carrying capacity** (K) for individuals. It will be a positive number and the population may grow if N is less than K, but it will decrease when N is larger than K, making I negative. There will be no growth and no decrease when N is equal to K, which is the state of equilibrium when a population has stabilized its size.

The typical r-strategist challenges the capacity of the population system. It has a short life cycle, becomes sexually mature at a young age and produces a large number of juveniles per individual parent. Its population will have a high reproductive potential producing a large number of juveniles within a short period of time. It gambles that most of the individuals will survive and succeeds when the death rate is low. When this occurs its population increases exponentially and can be described by a J-shaped curve (Figure 5.4). The strategy is good when the population's food resources are sufficient, but limitations may cause the population to crash. Lemming populations are typical r-strategists that are extremely successful in some years, but experience dramatic cases of **environmental resistance** when the plants lemmings eat mobilize production of anti-grazing toxins.

Environmental resistance regulates all populations and has complex factors, i.e., scarcity and competition for food, and high population densities that favor diseases and attract predators. K-strategists are sensitive to environmental resistance due to intrinsic properties selected by evolution. Typical K-strategists have few predators, long life spans, late sexual maturation and few offspring, which are given parental protection. Accordingly, birth and mortality rates are low making 'r' a small number. This situation stabilizes the population size at an appropriate level well below the range of the carrying capacity of the environment and can be described by a S-shaped curve (Figure 5.4). However, the carrying capacity is not constant but variable and may change with complex abiotic and biotic factors (Figure 5.4).

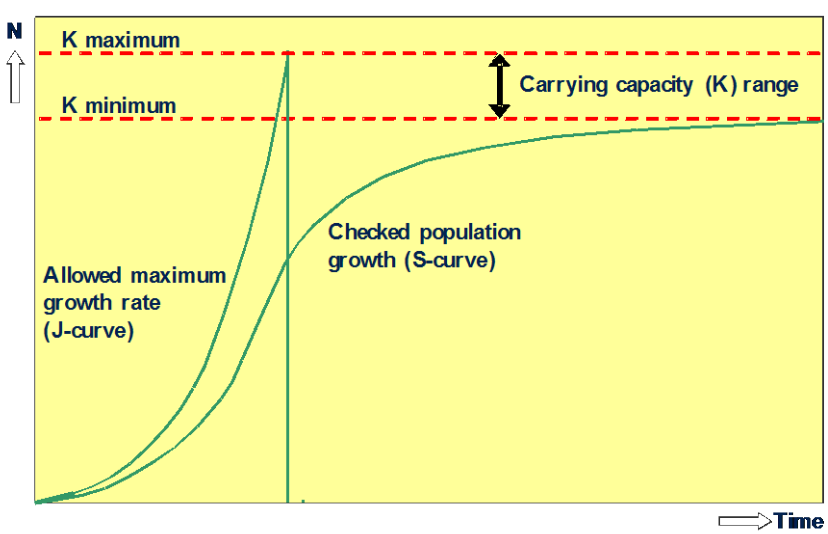


Figure 5.4. Population development may follow two strategic options.

Several arctic species display K-selective characteristics. One is the Arctic right whale known as the bowhead whale. It grows slowly to a maximum length of 25 m and sexually matures at around 25 years of age. It gives birth to one or two calves every third year, feeds them with milk and may live for more than 100 years. At the beginning of the 17th century a large population existed in the Greenland Sea, but industrial whaling introduced a new kind of environmental resistance that caused their extinction in the Atlantic sector of the Arctic. At the turn of the second millennium a few whales were observed near Svalbard possibly indicating a slow recovery. This whale stock remains critically endangered in Norwegian waters (CAFF, 2001).

In ecology a habitat refers to a place to live. Most populations occupy different habitats suited for particular parts of their life cycle. Fish leave feeding habitats when they congregate to mate in spawning habitats, while juveniles may be found in different habitats for growth into sexual maturity. Caribou populations migrate from forested wintering habitats in southern parts of their population systems, first to calving habitats on the tundra farther north and then to coastal Arctic landscapes where they gain strength for a new winter from rich grazing habitats.

Populations with many r-strategic properties may grow exponentially (J-curve) and break through the environmental carrying capacity of their system, which cause the populations to crash. Populations with more K-strategic properties are sensitive to complex environmental resistance and establish more stable populations (S-curve) that function within the limits of their ecosystem's carrying capacity.

In each of its habitats a particular population meets and interacts with populations of other species that may live there permanently or have migrated from places outside the population system of the particular population. A reproduction habitat for one population often overlaps with the feeding habitats of several higher-order predators that compete or interact in complicated predator-prey relations. Particular trophic interactions are often limited to small spaces and short seasons, for instance when migratory birds invade a resting place and feed for a day or two. Each temporal biota of organisms and their abiotic environment is an organismic system by definition.

**Learning Activity 2**

**Conduct a short literature search to discover examples of northern animal populations that have exceeded the carrying capacity of their habitats, resulting in environmental degradation. What factor or factors contributed to create these situations?**

## 5.5 Organism Interactions

An organismic system can be simple, such is the case within a bay where newly hatched fish larvae feed on the eggs and nauplii (larvae) of copepods, tiny crustaceans being part of the plankton moved around by currents. On land an organismic system could be a hill where a song-bird feeds its chicks with insect larvae picked from leaves of trees around its nest. These organismic systems disintegrate when the fish, copepods and song-birds finish their reproductive season and leave for different destinations. These examples illustrate organismic systems are not permanent. Some species that form the biota of the system may occur in the same season every year, but the numerical composition may not be the same. Many abiotic and biotic factors are independent or out of phase with each other and may vary in strength from year to year.

**Autecology** is a useful term for the study of an individual organism or a single species studied in isolation either in an experimental setup or in its natural environment without regard to other species. Such studies have established that some species are **eurytopic,** meaning that they tolerate considerable environmental variation on spatial and temporal scales. In contrast, **stenotopic** species require some environmental variables to be very stable at levels established by its genotypic capacities. The capacities of a species and the biological relationships between individuals of the same species are referred to as **intraspecific**.

The study of **interspecific** relations deals with how species interact with each other. **Synecology** is the science of how species function together within their biota. Synecological relationships may be very discrete and not obvious, while others may be very direct as in **symbiosis** where two species live together in a close and permanent relationship. Symbiosis appears in three forms:

1. **Mutualism** – beneficial to both species,
2. **Commensalism** – beneficial to the **symbiont** and presenting neither benefits nor harm to the host, and
3. **Parasitism** – beneficial to the parasite and harmful to the host.

**Learning Activity 3**

**Conduct a short literature search to identify examples of each form of symbiosis in circumpolar ecosystems.**

Organismic systems have no limits other than those appropriate for a study's purpose. Ecology is often studied in a particular **biotope** that contains a typical composition of species expected to be found associated with a particular abiotic environment. For example, a biotope may be a poorly drained lowland landscape characterized by sedge meadows where particular plants and insects are expected to occur. A biotope is permanent and recognizable while it may contain a conglomerate of smaller and characteristic biotas that change with the seasons. Biotopes may be grouped into larger **biomes** that are classified according to the dominant vegetation (see Module 6). The taiga is the northernmost biome of the Boreal region, a Subarctic biogeographic region dominated by evergreen coniferous trees. Farther north is tundra, a typical biome of the Arctic region. It is characterized by wetlands where underlying permafrost causes water to accumulate at the ground surface and the grasslands of polar steppes where precipitation, in the form of rain or snow, is in short supply throughout the year.

The Arctic drift-ice ecosystem may be classified as a marine biome because of its ice-algae, which form mats underneath the ice-floes in Arctic seas and are fed upon by crustaceans that are food for several marine predators. Another biome is the belt of intertidal seaweeds and subtidal kelp forests that grow along shores in the Boreal region. The rest of the marine environment poses a problem because the flora of the open sea consists of phytoplankton that grow and die within a short period when sufficient sunlight is available to facilitate photosynthesis. Many of these algal species are cosmopolitans moved around by ocean currents. Therefore, all open oceans and coastal seas of the world ocean should be considered a single biome. However, the physical geography of ocean basins varies considerably in relation to fresh water inputs, sea ice cover, bottom topography and geophysical processes, which govern and structure where and how marine microalgae grow (see Module 7).

The boreal and arctic regions contain species typical of each region and their stenotopic species never meet. However, some are more eurytopic and overlap in the **Subarctic Transitional Zone** (Figure 5.5). The subarctic transitional zone's demarcation lines are the northern limit of predominantly boreal species and the southern limit of predominantly arctic species. Species that occur only north of the subarctic are **endemic** to the arctic**.** Some species like capelin (a marine fish) are endemic to the subarctic. They and many other endemic species as well as boreal and arctic species occupy the transitional zone, which contributes to **species diversity** of sub-arctic organismic systems. **Biodiversity** is more than simply the number of species.

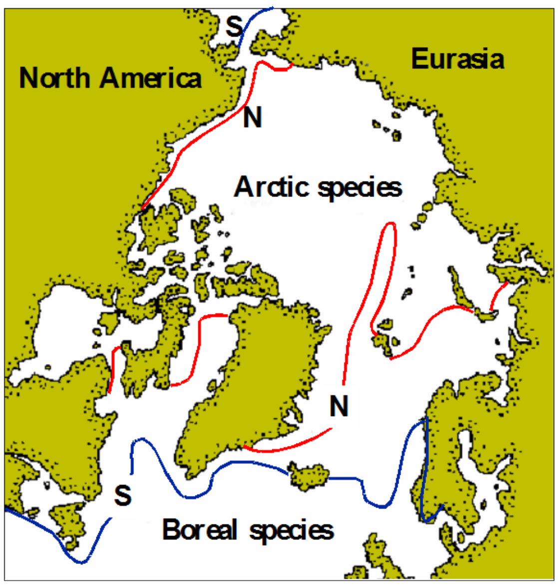


Figure 5.5. Zoogeographical distribution of marine animals.

N: Northern boundary of cold-adapted boreal species. S: Southern boundary of warm-adapted arctic species. The Subarctic transitional zone that is situated between the two borders contains endemic Subarctic species mixed with Arctic and Boreal species.

Biodiversity is more than simply the number of species. The Subarctic climate is variable over time scales ranging from months to millennia. Inhabitants of the Subarctic tend to be eurytopic with a wide intraspecific genetic capacity to manage changing climate and many ecological roles in an ecosystem. Biodiversity is the result of how populations function as reproductive units and their plasticity which generates phenotypes; what some authors call “ecotypes”.

## 5.6 Ecosystems Dynamics

### Food Webs

Ecosystems direct flows of energy and matter through **food chains** from the first trophic level of autotrophs up the chain of increasingly higher trophic levels of heterotrophs. Many animals feed on a variable diet that changes with time and body size, which causes energy and matter to follow a multitude of pathways through a **food web**, a network of interconnected food chains. Each individual operates within the food web of its population changing diet as it grows and visits the different habitats of its population system. Consider a food web that is established when an insect larva hatches from its egg in the spring and starts grazing on sprouting leaves of the subarctic tree its parent selected as a food source when it deposited its eggs. As the larvae grow in size some may fall prey to songbirds that exploit their breeding habitat to feed their chicks. After a few weeks the young birds are close to fully grown and leave the nest. Some may fall prey to local predators like young hawks being taught to hunt by non-migratory parents. Survivors may succeed in migrating south to wintering habitats where their biomass is fed into chains of different consumers and decomposing bacteria. In this case, the same tree would give rise to different food chains, one ending up in a non-migratory subarctic predator, while another demonstrates that any ecosystem leaks energy to other ecosystems.

Arctic plants are fed upon by first order consumers like insect larvae, lemmings or moose. None are very migratory and all become sexually mature at a young age. Lemmings may reproduce at a few weeks of age and a moose cow may be sired at an age of one year. Insects are usually one year old when they get wings and die after a brief mating season. Insect abundance and their high protein value is exploited by local shrews that eat more than their weight per day and by grouse chicks that turn into first order plant consumers after some weeks. Top predators of food chains on land are carnivorous mammals like wolves, wolverines, lynxes and foxes, and birds of prey like owls and eagles. All grow into adults within a year. Once reaching adulthood, consumers at high trophic levels may live for many years, but their life spans are not comparable with what is experienced in marine systems.

Open sea biological systems are different because producers are not long-lived plants rooted in one place. Producers are unicellular microalgae doubling their biomass in a matter of days by simple cell division in the upper few meters of the ocean where photosynthetic active radiation (PAR) is sufficiently strong. Dominating first order consumers are tiny crustaceans called copepods. Microalgae and their consumers are suspended in surface currents that transport them from one place to another usually over huge oceanic distances. Microalgae may aggregate into larger flocs that sink to the bottom to be eaten by animals that live on or in seafloor sediments or attached on rocky surfaces. In northern latitudes most marine animals living in deep water produce larvae that feed on microalgae in the sunlit upper layer of the ocean while currents carry them to distant destinations where they settle into an organismic system suited to their biological functions.

It should be evident that the first trophic levels of marine food chains operate in a three-dimensional space over vast areas and into the greatest depths, while food chains on land operate on smaller spatial scales. Nonetheless, it is a general principle that consumers at higher trophic levels tend to shift to larger food as they grow. They are forced to switch between food chains. Omnivores that have not developed a highly specialized feeding apparatus eat whatever is available or feasible. Examples are the brown bear that feeds on herbs and berries as well as on mice, moose and salmon, and the Arctic char that feeds on marine copepods as well as freshwater mollusks and fish in both environments. Both operate according to individual tactics within different food chains that are appropriate at a given time and situation, and are examples of how populations of species with wide fundamental niches may exploit extensive parts of an ecosystem's complex food web.

### Energy Flow

Biomass produced by autotrophs is stored in organic tissues and materials that represent potential energy and sources of biochemical matter that may be utilized by consumers. Potential energy passes through a food-web with considerable energy loss to the environment. Consumers leave remains from their meal in their habitat and discard significant amounts of biomass when feces are evacuated from their guts. Some digested biomass is rebuilt into new tissues and materials that are available for predators at the next trophic level. Approximately 90 percent of consumed energy from the lower trophic level is lost to the environment. This loss occurs as heat transferred to the environment through biochemical processes within the organism or through mechanical work on the physical environment (e.g., walking, swimming). Approximately ten percent of consumed energy stored in consumer biomass is available to the next trophic level as body tissues (Figure 5.6).

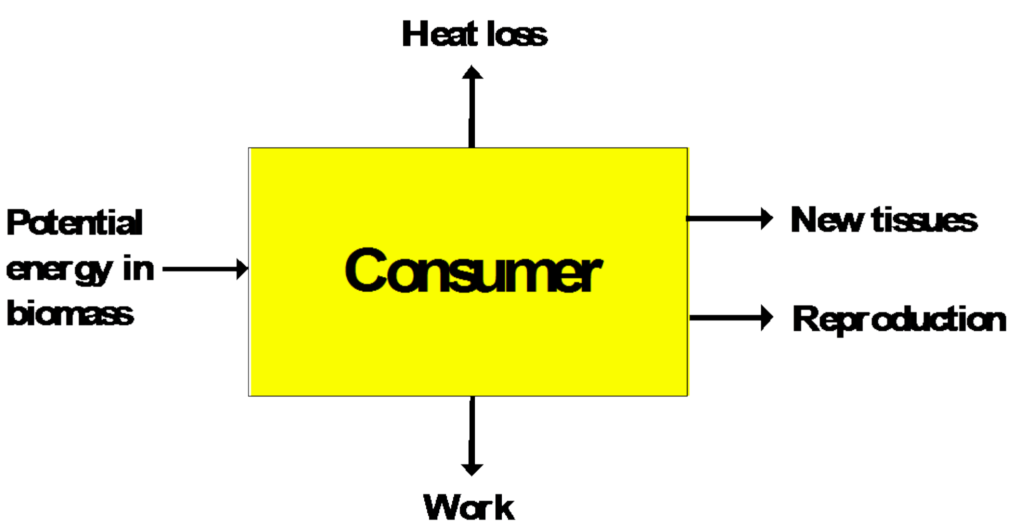


Figure 5.6. Energy use on the consumer trophic level. Only ten percent of available energy becomes available as food for a consumer at the next trophic level in terms of body tissues or reproduction products (semen, eggs, embryos).

At each trophic level the recombination of existing biomass into new growth and reproduction in consumer populations is hard work and requires energy. The energy is taken from the disintegration of biochemical molecules. The most complex molecules disintegrate into glucose and smaller components. Some components are not needed and even harmful if they accumulate in the organism. Animals discard ammonia, urea and other simple molecules stored in their ecosystem or recycled by autotrophs. The degradation of biomass and loss of matter to the environment makes a population produce less biomass than it takes from lower trophic levels.

Loss of energy from one trophic level to another is proportional to the difference in carbon stored as biomass at each level. Annual energy storage at the highest trophic levels is insignificant in terms of the overall energy budget of an ecosystem (Figure 5.7). Most energy in ecosystems serves to maintain producers and 1st and 2nd order consumers.

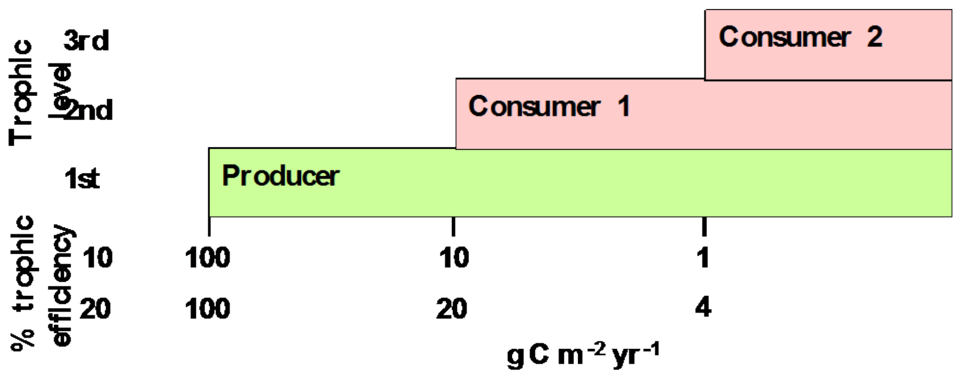


Figure 5.7. Carbon contained in biomass originally produced by autotrophs is reduced by the two lowest consumer levels, which is equivalent to the loss of 96 – 99 percent of stored energy depending on the trophic efficiency.

Energy loss to the environment applies equally to terrestrial and aquatic ecosystems. On land, warm-blooded mammals and birds maintain high body temperatures that make them active irrespective of ambient temperatures (**homeotherms**). These organisms lose considerable quantities of heat to the environment as water vapour from breathing (**latent heat**) and consume energy by being physically active. Fish and aquatic invertebrates are **poikilotherms**, meaning that their body temperature varies with their environment resulting in less direct heat loss than from homeotherms. Some fish may be active as they chase prey; however, more conservative energy use by aquatic organisms allows aquatic ecosystems to function with a higher **trophic efficiency** than terrestrial ecosystems. Higher trophic efficiency in poikilotherms may explain why aquatic food chains tend to be longer than terrestrial food chains where homeotherms operate on low trophic levels. Heat released by organisms is gradually dispersed within the abiotic parts of the ecosystem and eventually lost as infrared radiation from the biosphere.

## Biogeochemical Cycling of Matter

The global hydrological cycle distributes solar energy that maintains the ecological vigor of the biosphere. Water vapor is the globe's most important greenhouse gas. Water vapor's capacity to absorb infrared radiation emitted from the Earth's surface warms the atmosphere creating a comfortable environment for humans and other organisms (see Module 2). Most atmospheric water vapor originates from evaporation of seawater. Absorption of solar radiation loads energy into water molecules. It takes 560 calories (2272 J) of solar energy to evaporate one gram of water. This energy is released as latent heat when water vapor condenses to form precipitation. Precipitation as rain and snow over land supplies water to ponds, lakes and rivers. The runoff from land in northern latitudes is usually highly seasonal with typical late spring or early summer peaks in meltwater discharge (Figure 5.8). Freshwater discharge from continental watersheds mixes with seawater to form water masses and fronts that have important ecological functions in coastal seas (see Module 7). Living organisms would not exist in the absence of this liquid water.

Biogeochemical cycling involves the exchange of various atmospheric gas molecules that circulate with water vapour in the troposphere, the lowest 8 – 15 km thick layer of the atmosphere. The troposphere contains about 21 percent oxygen ($O_2$), 78 percent nitrogen ($N_2$) and 0.03 percent carbon dioxide ($CO_2$). Standing crops of autotrophs, as well as biomass stored in peat and coal, and oil and gas mineral reserves account for the disproportion between carbon dioxide and oxygen. Nitrogen is not directly used by producers but some soil-dwelling bacteria use a small proportion for production of nitrate ($NO_3^-$), an essential nutrient for autotrophs.

Liquid water facilitates the chemical weathering of rocks releasing essential inorganic nutrients into surface waters and groundwater where they are accessible to autotrophs. Calcareous rocks are easily eroded and produce "hard water" that contains calcium ($Ca^{2+}$). Calcium is widely used by marine organisms to produce calcium carbonate ($CaCO_3$) in seashells and calcium phosphate, as the mineral apatite ($Ca_5(PO_4)_3F$), in vertebrate bones. Following the death of organisms these materials accumulate in the biosphere to form sediments that are gradually transformed by geological processes to form rocks like limestone and marble ($CaCO_3$), and apatite which are mined for industrial production of fertilizers (see Sedimentary Rocks in Module 3). These minerals are typical examples of the cycling of materials between the Earth's crust, surface water, groundwater and organisms (Figure 5.9). Some sedimentary rocks contain coal, oil and gas derived from the geological transformation of organic matter. Human exploitation of these non-renewable natural resources is a contributing factor to climate change and environmental problems related to industrial pollution throughout the circumpolar North.

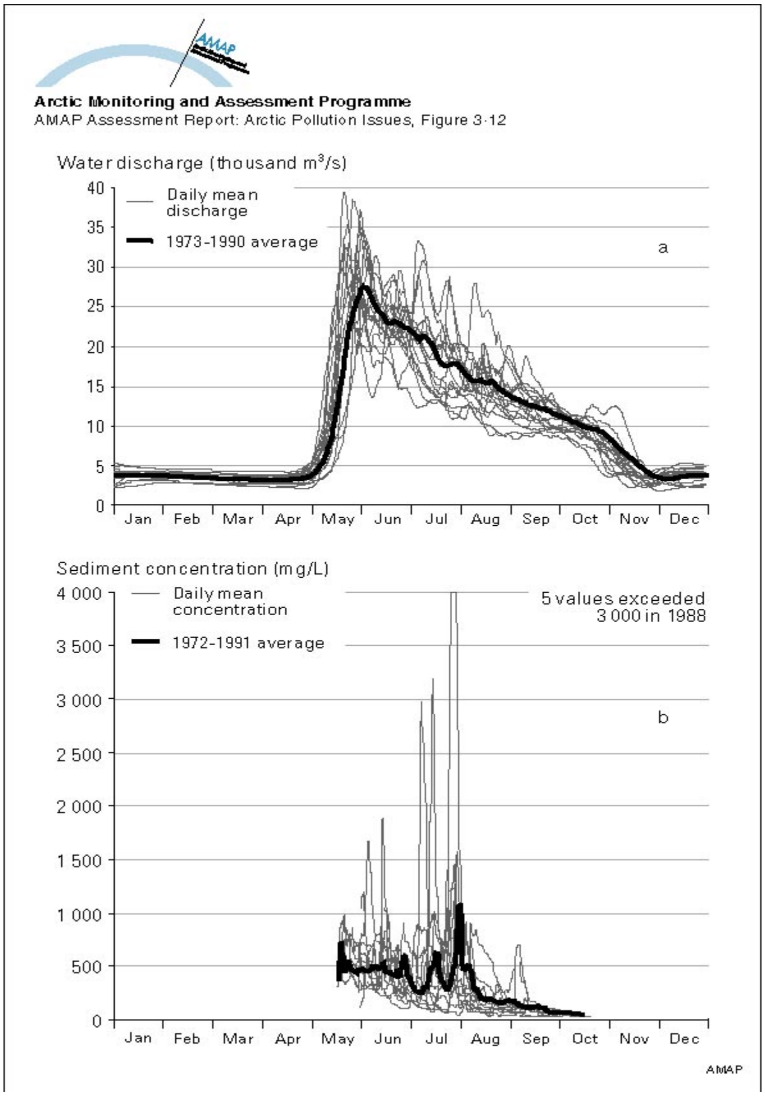


Figure 5.8a. The annual (1973-1990) and mean annual hydrographs for the Mackenzie River above the Arctic Red River, NWT, Canada, indicating the dominance of the spring freshet in May; b. Daily suspended sediment concentrations (mg/L) and mean annual suspended sediment concentrations (1972-1991) for periods of high flow and high sediment concentration in the Mackenzie River above the Arctic Red River. HYDAT, 1994. Hydrology Data Base, version 4.94. Environment Canada, Ottawa, Canada. Cartographer/Designer and Graphical production: Philippe Rekacewicz and Emmanuelle Bournay (GRID-Arendal).

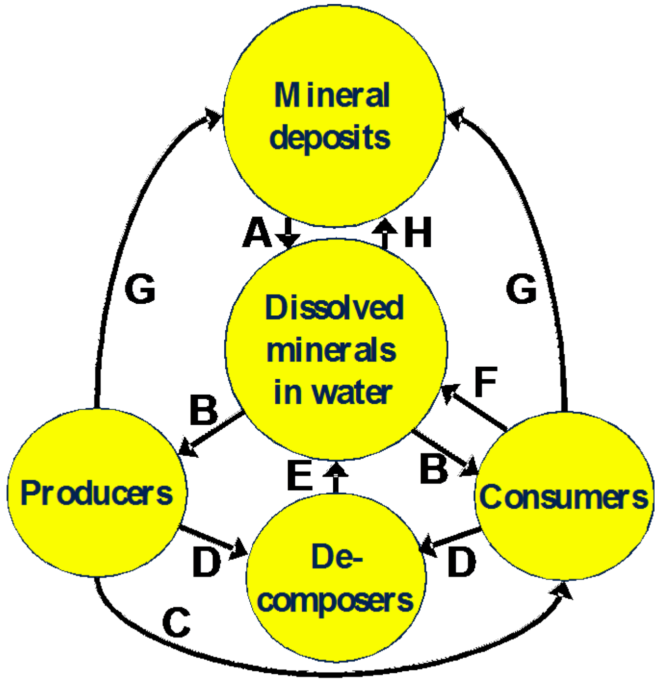


Figure 5.9. General flow of minerals between food webs and their abiotic environments of solid and dissolved matter. A) Chemical and bacterial weathering of rocks, sediments and soil. B) Uptake from soil water or aquatic habitat. C) Consumption of biomass. D) Decomposition of biomass. E) Mineralization of biochemical molecules. F) Evacuation of soluble minerals in feces and urine. G) Mineralization of organic matter. H) Flocculation and sedimentation of mineral particles.

**Learning Activity 4**

**The rate at which biogeochemical processes operate at Earth's surface is influenced by ambient temperatures and the availability of moisture at and below the ground surface. Review the materials related to temperature and precipitation presented in Module 2. How do these climatic variables influence the production and availability of inorganic plant nutrients in northern soils?**

## Establishment and Handling of Control Systems

In the absence of environmental resistance any population of organisms has the potential to increase beyond the carrying capacity of its ecosystem. A process that reduces the resistance is a signal that allows growth. The resistance can be a shortage of food or the presence of predators, sometimes in combination, both being part of a complex of factors that regulate the ecosystem. In many places wolves have been

extinguished by human predator control, which usually causes prey populations (e.g., deer, moose) to increase providing more game for hunters. Populations not preyed upon by wolves often grow out of proportion with their grazing habitat's carrying capacity and may crash due to hunger and contagious diseases. Humans are not able to cull sick and genetically weak animals with the same precision as natural predators because hunters prefer to harvest healthy animals. The present reindeer husbandry in Arctic Norway has developed into an industry characterized by overpopulation, overgrazing and diseases causing a suboptimal economic outcome. Exclusive human exploitation is an inadequate replacement of environmental resistance played by wolves and other predators that tend to keep prey populations healthy and below the carrying capacity of grazing habitats. It may be speculated that ecological stability can be acquired in systems where natural predation works in concert with human management practices that focus on sustainable yields by setting limits for total allowable harvests.

Some control mechanisms are sophisticated. Predators may keep stocks of producers or consumers at levels that permit high biodiversity. One keystone species is the Alaska sea otter that feeds on a wide range of marine animals including sea urchins. Centuries of fur trade resulted in the serious reduction of the sea otter population, which may have caused sea urchins to overgraze kelp beds that are part of a biota characterized by high species diversity. However, the absence of sea otters in many regions also caused populations of crabs and other human resources to increase for the benefit of commercial fishing. Management of sea otter hunting caused sea otters to return to their original habitats resulting in reduced quantities of marine organisms available for exploitation by fisheries communities. This case shows that management practices may improve biodiversity and ecological stability at the cost of sector economies.

### Development of Biodiversity

Biodiversity in any biota is the result of previous and ongoing evolution that operates to improve flows of energy and matter within its ecosystem. It is the biotic interaction between an ecosystem's populations and the effects of their environment that continuously select for new ecological capacities. They arise from **mutations**, the recombination of genetic codes in individual organisms. If it represents an improvement in the organism's **adaptation** to abiotic or biotic challenges posed by the ecosystem, the population may over time reproduce it as a major character (according to the theory of **natural selection** developed by Charles Darwin (1809-1882)).

Adaptations that make populations fit for their environment occur at three levels:

1. **Acclimation** or short-tem adjustment in eurytopic species that can mobilize and reverse physiological functions. A typical example is the ability of some fish to migrate between lakes and the sea.

2. **Ontogenetic** regulation, a life-long individual ability induced by the environment. For example, fish eggs exposed to low temperature cause the embryo to develop extra vertebrae (segments) in its backbone, which cannot be reversed.

3. **Phylogenetic** fixation due to a change in the genetic code at the expense of flexible acclimation and ontogenetic regulation, which may occur in a stable environment that does not require ecological flexibility in a particular capacity.

A biological species may have a wide **fundamental niche**, meaning it can tolerate a wide range of environmental conditions frequently due to a combination of flexible acclimation, ontogenetic potentials and phylogenetic complexity. Their populations are capable of occupying wide geographic areas where the ecological conditions vary over distances and time. Species with great capacity to adapt are eurytopic in contrast to stenotopic species that have specific requirements and demand a stable environment. A wide fundamental niche may cause a species to establish a multitude of populations. They can be recognized by their different genotypic constitutions (genome structure, DNA bar-code) that are required for the occupation of particular habitats, such as with Atlantic cod. Each has a realized niche that is less than the fundamental niche of the species. However, environmental differences within a single population system may offer sites that are habitable for some individuals but not tolerated by others. This kind of environmental restraint within population systems is called phenotypic selection and is important to evolution when phenotypes become isolated. Sometimes phenotypes may be recognized as morphs that display morphological features different from the rest of their population. It is expressed in populations of Arctic char, for example, where some fish have large jaws and teeth fit for predatory or cannibalistic roles.

Traditionally biodiversity is usually attributed to the number of species in an area. Today DNA bar-coding is increasingly used to study genetic diversity within species and populations. Whether the biodiversity is interspecific within a community or intraspecific within a species it adds to the feedback processes that regulate the state of equilibrium in an ecosystem. Species of the Arctic region generally have to respond to an extremely variable physical environment, both seasonally and inter-annually. Arctic species therefore tend to possess wide fundamental niches and acquire ecological plasticity from acclimation and ontogenetic regulation. This differs from tropical rainforests, coral reefs or the Antarctic ecosystems that have relatively stable climates and species with narrow fundamental niches.

Several ecological feedback processes may regulate species richness. High abiotic diversity may establish a habitat richness that favors the presence of many species, e.g., rocky tidal shores. Crevices and stones provide hiding places and variables like thermal exposure, desiccation and the duration of the feeding period, which changes over short vertical distances. Where abiotic conditions are more stable competitive species may establish **climax communities** of uniform biota, e.g., in the taiga. This spruce forest is poor in species. Disturbances such as wildfires, high winds, heavy snow falls, intense forestry and larval infestation of parasitic insects create open clearings that attract opportunistic plants and animals. The first invasion may be a massive occurrence of a few species, but they are gradually replaced by other species that increase biodiversity. Spruce that grow slowly but tall eventually gain supremacy over less competitive plants. They take control over space, sunlight and nutrients causing the biota to become poorer in species. The development is understood as **ecological succession** and terminates in a climax community that is stable and self-perpetuating.

## Conclusion

This module has focused on the transformation and exchange of matter and energy within biotic communities.  The processes of photosynthesis and chemosynthesis facilitate the production of organic materials by autotrophic organsims. These organic materials are subsequently consumed by heterotrophic organisms to support their growth. The  tissues of both autotrophic and heterotrophic organisms are eventaully consumed by detritivores or decomposers. These organisms are responsible for the break down of organic matter and the release of inorganic molecules, facilitating the recylcing of these nutrients to autotrophic organisms. The rates at which matter and energy are transformed and exchanged within food webs or food chains is influenced by physical and chemical variables in the environment, as well as the population dyanmics of the various organisms present within a biotic community.

Organisms are constantly interacting with one another and the environment that they inhabit. Interspecific interactions may involve organisms that live together in a close and permanent relationship referred to as symbiosis. Some of these interactions are mutually beneficial: however, parasitism confers benefits to the parasite while proving harmful to the host organism. At a larger scale, an organism's capacity to adapt to changes in both abiotic and biotic elements in the environment influences the size of the fundamental niche that it occupies. Eurytopic organisms inhabit large fundamental niches; they are adapted to occupy wide geographic areas in which environmental conditions vary over distance and time. On the other hand, stenotopic organisms occupy relatively restricted geographic areas generally characterized by stable environmental conditions. Arctic species tend to possess wide fundamental niches in contrast to the narrow fundamental niches occupied by many Antarctic species.

## Discussion Questions

1. Discuss criteria that limit the spatial dimensions of population systems and explain why ecosystems are larger than populations systems.
2. How may food webs, energy flow, cycling of matter and control systems interact with biodiversity?
3. Discuss major differences between terrestrial and marine ecosystems.

## Study Questions and Answers

1. What distinguishes an ecosystem from an organismic system?

   Answer: An ecosystem is the conceptual model of a geographical space where a community of consumer and decomposer populations digests nearly all biogenic energy contained in biomass produced by the ecosystem's populations of autotrophs. Although the food-web may be subject to interannual changes, conservation of energy within spatial dimensions of the ecosystem allows predictable and accountable energy budgets that can also be simulated by numerical modelling on annual and interannual scales. An organismic system is a temporary biota that functions as a common habitat for organisms representing some of the different populations that make an ecosystem. Organismic systems import and export biomass by seasonal migration or transport by abiotic forcing, which is often highly variable making energy budgets unpredictable on a temporal scale.

2. Suggest two cases of food-chains that demonstrate conservation of energy within a biome and two that demonstrate leakage of energy between biomes.

   Example: Birch leaves grazed by insect larvae are preyed upon by juvenile migratory songbirds. Some fall prey to local owls and others to predators in their wintering habitats on lower latitudes.

3. How may abiotic variables interact with growth in populations of herbivorous poikilotherms?

   Examples:

   - Their metabolism increases with temperature.
   - Temperature regulates the seasonal growth of food.
   - The salinity of seawater prevents stenotopic freshwater species from feeding on marine biomass.

4. List biological features that distinguish r-strategists from K-strategists.

   Answer:

   - r-strategists are small, have short generation times, produce many eggs at a young age and do not protect their progeny.
   - K-strategists are large, become sexually mature at high age, produce few offspring and protect their progeny.

5. How may the balance between eurytopic and stenotopic species influence the biodiversity of an organismic system?

   Answer: Eurytopic species have wide fundamental niches and may play ecological roles that compete with several stenecous species with narrower fundamental niches. Stenotopic species require very specific environmental conditions that optimize their competitiveness. Abiotic conditions must be stable to allow for a rich biota with many stenotopic species.

6. Select a typical Arctic organismic system and discuss how the five functional components of the larger ecosystem cause its biodiversity to change with the seasons.

   Example: Many consumers leave the northern birch forests when low temperature and short days causes the plants to shed their foliage. The leaves are left on the ground to be decomposed by fungi and bacteria, but the mineralization stops when the soil water freezes. The inorganic nutrients are stored until the spring thaw makes them available for plant roots, which allow trees and herbs to grow new leaves. The forest biodiversity increases when invertebrate eggs hatch into larvae and herbivorous and carnivorous consumers migrate into forest habitats from different winter habitats to feed and breed. In contrast the forest biota becomes less diverse during winter when only stationary consumers are present, constituting a much simpler food-web.

## Glossary of Terms

**Abiotic:** Not associated with or derived from living organisms. Abiotic factors in an environment include such items as sunlight, temperature, wind patterns, and precipitation.

**Acclimation:** Any of the numerous gradual, long-term responses of an organism to changes in its environment.

**Adaptation:** the evolutionary process whereby an organism becomes better able to live in its habitat or habitats.

**Autecology:** The branch of ecology that deals with the biological relationship between an individual organism or an individual species and its environment.

**Autotroph:** An organism that produces complex organic compounds (such as carbohydrates, fats, and proteins) from simple substances present in its surroundings, generally using energy from light (by photosynthesis) or inorganic chemical reactions (chemosynthesis).

**Biomass:** Biological material from living, or recently living organisms: alternatively, the total mass of living matter within a given unit of environmental area.

**Biome:** A major regional or global biotic community, such as a tundra or taiga, characterized chiefly by the dominant forms of plant life and the prevailing climate.

**Biosphere:** the global ecological system integrating all living beings and their relationships, including their interaction with the elements of the lithosphere, hydrosphere and atmosphere; also be called the zone of life on Earth.

**Biota:** The combined flora and fauna of a region.

**Biotic:** Associated with or derived from living organisms. The biotic factors in an environment include the organisms themselves as well as such interactions as predation, competition for food resources, and symbiotic relationships.

**Biotope:** A usually small or well-defined area that is uniform in environmental conditions and in its distribution of animal and plant life.

**Carnivore:** an organism that derives its energy and nutrient requirements from a diet consisting mainly or exclusively of animal tissue, whether through predation or scavenging.

**Carrying Capacity:** The carrying capacity of a biological species in an environment is the maximum population size of the species that the environment can sustain indefinitely, given the food, habitat, water and other necessities available in the environment.

**Chemotroph:** An organism (typically a bacterium) that obtains energy through achemical process, which is by the oxidation of  electron donating molecules (e.g. iron ($Fe^{3+}$), sulfur ($S^{2-}$), or ammonia ($NH_3$)) from the environment, rather than by photosynthesis.

**Climax Community:** An ecological community in which populations of plants or animals remain stable and exist in balance with each other and their environment. A climax community is the final stage of succession, remaining relatively unchanged until destroyed by an event such as fire or human interference.

**Commensalism:** in biology, a relation between individuals of two species in which one species obtains food or other benefits from the other without either harming or benefiting the latter.

**Community:** A group of interdependent organisms living and interacting with each other in the same habitat.

**Consumer:** An organism that generally obtains its food by feeding on other organisms or organic matter due to lack of the ability to manufacture its own food from inorganic sources sources; a heterotroph.

**Decomposers:** An organism whose ecological function involves the recycling of nutrients by performing the natural process of decomposition as it feeds on dead or decaying organisms.

**Detritivore:** Heterotrophic organisms that obtain nutrients by consuming detritus (decomposing plant and animal parts as well as organic fecal matter).

**Ecological Resilience:** In ecology, resilience is the capacity of an ecosystem to respond to a disturbance by resisting damage and recovering quickly.

**Ecological Succession:** The phenomenon or process by which an biotic community undergoes more or less orderly and predictable changes following disturbance or initial colonization of new habitat.

**Endemic:** A species observed uniquely within a defined geographic location or habitat type.

**Environmental Resistance:** The resistance presented by the environmental conditions to limit a species from growing out of control or to stop them from reproducing at maximum rate.

**Eurytopic:** Able to adapt to a wide range of environmental conditions; widely distributed. Used with reference to both plants and animals.

**Extirpation:** To destroy or remove completely a species from an particular area, region, or habitat.

**Food Chain:** The sequence of transfers of matter and energy from organism to organism in the form of food.

**Food Web:** A complex of interrelated food chains in a biotic community.

**Fundamental Niche:** The full range of environmental conditions and resources an organism can possibly occupy and use, especially when limiting factors are absent in its habitat.

**Habitat:** A place where an organism or a biological population normally lives or occurs.

**Herbivore:** An organism that consumes vegetation as its primary food source.

**Heterotroph:** An organism that consumes other organisms in a food chain. In contrast to autotrophs, heterotrophs are unable to produce organic substances from inorganic ones. They must rely on an organic source of carbon that has originated as part of another living organism. Heterotrophs depend either directly or indirectly on autotrophs for nutrients and food energy.

**Homeotherm:** An organism, such as a mammal or bird, having a body temperature that is constant and largely independent of the temperature of its surroundings.

**Interspecific versus intraspecific:** Interspecific competition, in ecology, is a form of competition in which individuals of different species compete for the same resource in an ecosystem (e.g. food or living space). The other form of competition is intraspecific competition, which involves organisms of the same species.

**Keystone Species:** A species that has a disproportionately large effect on the communities in which it occurs. Such species help to maintain local biodiversity within a community either by controlling populations of other species that would otherwise dominate the community or by providing critical resources for a wide range of species.

**K-Strategist:** Species that display traits associated with living at densities close to carrying capacity, and typically are strong competitors in such crowded niches that invest more heavily in fewer offspring, each of which has a relatively high probability of surviving to adulthood.

**Mutation:** A change of the DNA sequence within a gene or chromosome of an organism resulting in the creation of a new character or trait not found in the parental type.

**Mutualism:** A symbiotic relationship between individuals of different species in which both individuals benefit from the association.

**Omnivore:** Organisms that eat both plant and animal material as their primary food sources.

**Ontogenetic:** related to the the origin and development of an individual organism from embryo to adult.

**PAR (Photosynthetically Active Radiation):** defines the range of wavelengths of solar radiation from 400 to 700 nanometers that photosynthetic organisms are able to use in the process of photosynthesis.

**Parasitism:** A form of symbiosis in which one organism (called the parasite) benefits at the expense of another organism usually of different species (called the host). The association may also lead to the injury of the host.

**Photosynthesis:** The synthesis of complex organic material using carbon dioxide, water, inorganic materials, and solar energy captured by light-absorbing pigments, such as chlorophyll.

**Phototroph:** An organism that obtains energy from sunlight for the synthesis of organic compounds.

**Phylogenetic:** the sequence of events involved in the evolution of a species or higher taxonomic grouping of organisms.

**Poikilotherm:** An organism, such as a fish or reptile, having a body temperature that varies with the temperature of its surroundings.

**Population:** A group of organisms of one species that interbreed and live in the same place at the same time.

**Primary Production:** Primary production is the production of organic material from atmospheric or aquatic carbon dioxide. It may occur through the process of photosynthesis, using light as a source of energy, or chemosynthesis, using the oxidation or reduction of chemical compounds as a source of energy.

**Producer:** An organism (primarily green photosynthetic plants) that utilizes the energy of the sun and inorganic molecules from the environment to synthesize organic molecules. Respiration: The process by which animals use up stored foods (by combustion with oxygen) to produce energy.

**R-Strategist:** Species are those that place an emphasis on a high growth rate, and typically exploit less-crowded ecological niches and produce many offspring, each of which has a relatively low probability of surviving to adulthood.

**Secondary Production:** Secondary production represents the formation of living mass of a heterotrophic population or group of populations over some period of time. It is the heterotrophic equivalent of net primary production by autotrophs.

**Species:** In biology, a species is one of the basic units of biological classification and a taxonomic rank. A species is often defined as a group of organisms capable of interbreeding and producing fertile offspring.

**Species Diversity:** The number and variety of species present in an area and their spatial distribution.

**Standing Crop:** The standing crop is the quantity or total weight or energy content of the organisms which are in a particular location at a particular time.The standing crop is the total dry weight of all organisms.

**Standing Stock:** A species, group or population of organisms that maintains and sustains itself over time in a definable area.

**Stenotopic:** An organism able to tolerate only a restricted range of habitats or ecological conditions.

**Symbiosis:** Symbiosis is a close ecological relationship between the individuals of two (or more) different species.

**Synecology:** The branch of ecology that deals with the ecological interrelationships among communities of organisms.

**Tipping Point:** In ecology, the time at which a change or an effect cannot be stopped.

**Trophic Efficiency:** A measure of the amount of energy in the biomass that is produced by one trophic level and is incorporated into the biomass produced by the next (higher) trophic level.

## References


Lovelock J 2006. The Revenge of Gaia. Allen Lane, London. 177 pp.

Odum EP and GW Barrett 2005. Fundamentals of Ecology. Thomson Brooks/Cole, Belmont, California. 598 pp.

Odum HT and MT Brown 2007. Environment, Power and Society for the Twenty-First Century. Columbia University Press, New York. 432 pp.

Ricklefs RE. 1990. Ecology. W.H. Freeman, New York. 896 pp.


## Supplementary Resources


CAFF. Arctic Flora and Fauna, Status and Conservation. Edita, Helsinki, 272 pp.

http://arcticportal.org/arctic-council/working-groups/caff-document-library/arctic-flora-and-fauna/.

Encyclopædia Britannica, Inc. 2009. http://info.eb.com/index.html.