

2 Ecology

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Abstract: Ecology is a science that studies the interactions between organisms and their environment. The fundamental subject of interest in ecology is the individual organism. Topics of interest to ecologists include the diversity, distribution and number of particular organisms, as well as cooperation and competition between organisms, both within and among ecosystems. Today, ecology is a multidisciplinary science. This is especially true when the subject of interest is the ecosystem or biosphere, which requires the knowledge and input of biologists, chemists, physicists, geologists, geographers, climatologists, hydrologists and many other experts. Ecology is applied in the science of restoration, repairing disturbed sites through human intervention, in natural resource management, and in environmental impact assessments.

Keywords: elements of ecology, environment, habitat, biodiversity

2.1 Introduction

The term ecology is frequently used today and has a broad meaning. Ecology is referred to as a science, as nature, as an idea and as a movement. In this chapter, ecology refers to the scientific study of the mutual interactions between organisms and their environment. For practical reasons, ecology is typically divided into plant ecology, animal ecology and human ecology. One of the first to highlight the significance of ecological observations was the renowned natural historian Charles Darwin, in his book *On the Origin of Species* [1]. Darwin provided numerous examples of evolution (adaptation, natural selection, struggle for survival and extinction of species), which included a wide range of mutual relationships between organisms and their interactions with environmental conditions. The word ecology (Greek: *oikos* = house, home, habitat; *logos* = study, knowledge) was first coined by the German biologist Ernst Haeckel in his book *Generelle Morphologie der Organismen* [2].

The fundamental subject of interest in ecology is the individual plant or animal organism. Individuals of plants or animals do not live in isolation but are typically grouped, and such groups of similar individuals are called species. Although biologists have not agreed on a single definition of species, most accept that species are groups of individuals sharing similar morphological and genetic traits, and individuals of a species are able to reproduce with one another and produce fertile offspring. Today, ecology is a multidisciplinary science; to answer many of the questions this field addresses, cooperation from many different disciplines is required. This is particularly true when the subject of interest is the ecosystem or biosphere, which requires the knowledge and input of

biologists, chemists, physicists, geologists, geographers, climatologists, hydrologists and many other experts.

Humans, in addition to consuming vast amounts of energy, have polluted nature with industrial waste, harmful gases, pesticides, heavy metals and organic compounds, drastically reducing the diversity of plant and animal species and altering the ecological balance. The changed environment negatively affects human health and is gradually threatening human survival (climate change, greenhouse effect, destruction of the Earth's ozone layer). Industry, the foundation of global prosperity, has created significant global threats to humanity's continued survival. Therefore, future development should be based on environmental protection through sustainable development and management. This means that the use of natural resources must be sustainable, allowing those resources to regenerate and remain in ecological balance. By mastering the fundamental principles of ecology, we can more easily create the conditions for the rational use of the biosphere's natural resources, and improve relations between humans and their natural environment.

2.2 Conditions for life

Many factors influence the distribution and survival of species. Generally, these can be divided into abiotic factors – those of the non-living environment – and biotic factors – those of the living environment. The habitat, or biotope, as the area where a given species lives, is characterised by a specific and complex set of ecological factors. None of these factors acts alone, so organisms are distributed only in areas where the gradients of specific factors overlap in a suitable way. The range of fluctuation of a single ecological factor within which the life of a particular organism is possible, is called ecological valence (Shelford's law of tolerance) (Figure 2.1). However, if the effect of one ecological factor falls outside the limits of ecological valence, the organism could not survive. For each ecological factor, there is an optimal range, as well as a minimum and maximum. At both the minimum and maximum, the intensity of the ecological factor corresponds to the stress zone, or area pessimum (from Latin *pessimus* – very bad). The optimum is the quantity or intensity of the ecological factor that is most suitable for the organism, resulting in its maximal growth and development. The concept of the limiting effect of an ecological factor was introduced in ecology by V. E. Shelford [3], and it applies to all ecological factors and all organisms.

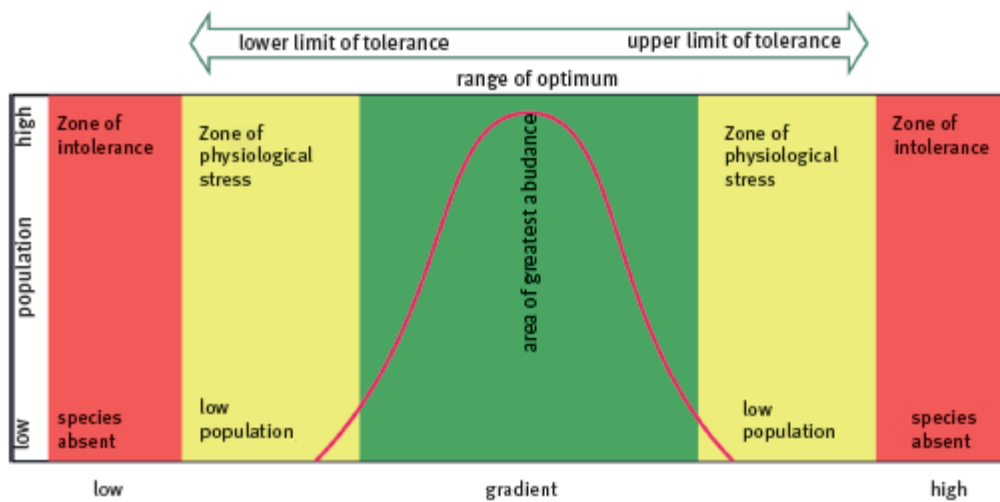


Figure 2.1: A schematic representation of ecological valence [inspired by [4].

Organisms with a wide range of tolerance for an ecological factor are called eurivalent species, while those with a narrow range of tolerance are called stenovalent species. Interestingly, a single life factor at its minimum can exclude a species from a given habitat, even if all other factors are within optimum ranges.

2.2.1 Abiotic factors

Temperature and moisture are key ecological factors that determine the distribution and development of plants. Based on these factors, we can distinguish different vegetation zones on Earth. For animals, vegetation is important as both shelter and a source of food. In areas where ecological conditions are unfavourable and plant cover is poorly developed, the diversity and abundance of animals are also lower due to the scarcity of suitable shelters and available food. Many animals are distributed only within certain temperature limits suitable for their survival, and the distribution of climate zones on Earth acts as a barrier to their wider dispersal. Monkeys and parrots are primarily distributed in the tropical and subtropical zones, while the polar bear, walrus and some diving birds are distributed in the polar regions. Another important ecological factor is light. The rhythmic change of light is essential for many daily and seasonal phenomena and activities in plants and animals. Day length determines when leaves begin to fall in many deciduous tree species in temperate climate zones. There are long-day and short-day organisms. For example, barley is a long-day plant and blooms under long-day light, while in tobacco, long days prevent blooming. Constant daylight is the reason why plants in the tropics bloom year-round, and why polar plants fail to thrive in other parts of the world, as they are adapted to long days. Trout spawn at a temperature of 6 – 7 °C (winter), although spawning can be induced experimentally at higher temperatures (summer) simply by reducing the amount of daylight. Shortening daylight also stimulates migrating birds to fly south. How organisms respond to rhythmic changes in the light intensity – day and night – is of particular ecological importance. Among mammals in temperate forests, 30–40 % are active during the day and 60–70 % are active at night. The distribution of animals also depends on light.

For example, in Norway, the wood mouse (*Apodemus sylvaticus*) reaches a maximum latitude of 62°N. This is due to the duration of the summer nights, which in that region last only 5 hours. As the wood mouse is nocturnal animal (active and feeding at night), a shorter night is one of the main reasons it cannot disperse further north; during such short nights, it simply cannot feed enough to ensure its survival.

Specific behaviour patterns are also linked to changes in photoperiod and temperature, such as bird migrations.

In aquatic ecosystems, primary producers (phytoplankton, macrophytes and seagrasses) are limited by the depth of light penetration, water temperature and the quantity of available nutrients, while for animals, the quantity of metabolic gases (oxygen and carbon dioxide), salinity and pressure (in the sea) are important factors.

2.2.2 Biotic relationships

Population

The living area of a species consists of many intertwining abiotic factors that affect the organism. However, individuals of the same species as well as those of other species, also come into contact and affect one another. A population is a group of individuals of the same species in a given area. Each population has its own dynamics and properties: population size, spatial distribution, age structure, sex ratio, birth rate, death rate, immigration rate and emigration rate. The spatial distribution of individuals in the environment may be caused by the distribution of resources or by social relationships among individuals.

Mutual interactions and relationships between individuals of the same species are called intraspecific relations. If a resource essential for the population's survival is limited, competition will arise among its members (intraspecific competition), which can restrict the population size. When ecologists study endangered species, the size of the surviving population is crucial for designing appropriate management strategies. Population size also depends on other characteristics: natality, mortality, survivorship, reproductive potential and dispersion. Populations increase through the birth of new individuals (natality) and the arrival of new individuals (immigration), and decrease through death (mortality) and individuals leaving the population (emigration).

Population growth can be exponential or logistic. Exponential population growth is characteristic of invertebrates and some vertebrates (such as rodents) when colonising new habitats, where the two most important resources – space and food – are not yet limiting (Figure 2.2). However, no real population can continue increasing exponentially for long and is instead stabilised at a certain level.

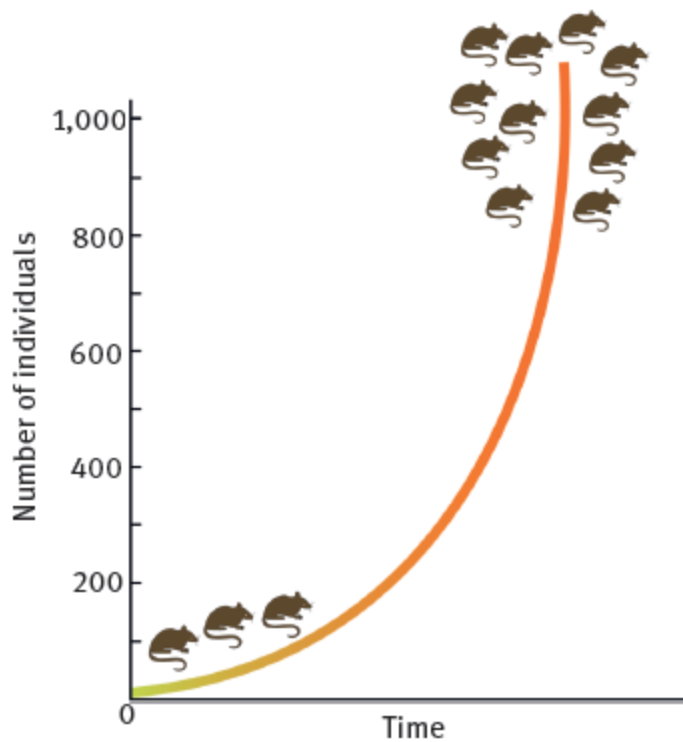


Figure 2.2: The exponential growth curve [inspired by [5].

Logistic growth results from limited resources in the habitat. It is characterised by the carrying capacity (K) of the environment, which indicates the maximum population size the habitat can support with its resources. For example, sheep introduced to the Australian island of Tasmania in 1800 experienced rapid population growth to almost two million individuals. This led to intense competition for food, and by 1885, their numbers had declined and stabilised at about 1.6 million individuals (Figure 2.3).

The terms r -selection and K -selection have been used by ecologists to describe the growth and reproductive strategies of various organisms. The r and K classification was originally proposed by R. McArthur and O.E. Wilson [6]. R -selected species inhabit variable, unstable habitats, while K -selected species occupy stable environments. Small body size, early reproductive maturity, high fecundity and low parental investment are the main characteristics of r -selected species. Flies and most invertebrates are examples of r -selected species. In contrast, K -selected species have low fecundity and high parental investment. Most mammals are examples of K -selected species.

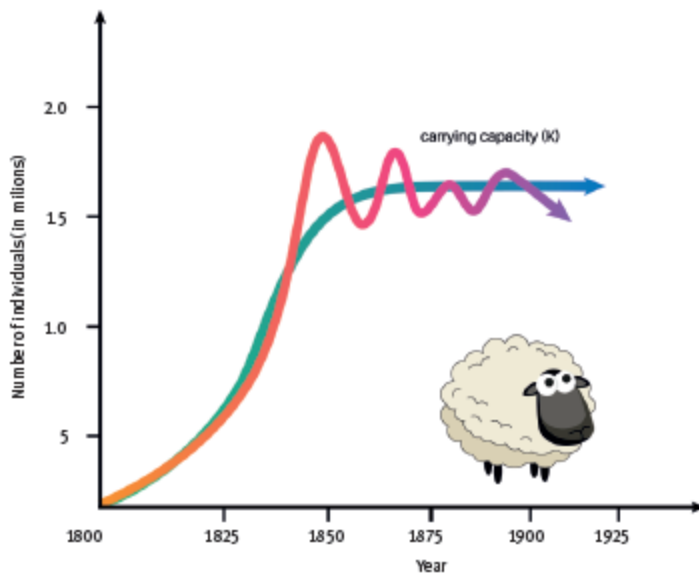


Figure 2.3: The logistic growth curve: when the carrying capacity is reached, there is no further increase in density [inspired by [5].

2.2.2.1 Interspecific relationships

Relationships between different species (populations) are called interspecific relationships and involve a range of mutual influences, such as competition, predation, parasitism, mutualism and commensalism. For example, one species may feed on another and is therefore dependent on it.

Competition

Species can compete for the same food source or space, and thus are in competition. An interesting example is the barnacles *Chthalamus stellatus* and *Semibalanus balanoides*. Both species inhabit the tidal zone, though *Chthalamus* is always found in higher areas and *Semibalanus* in lower areas of that zone. Connell [7] conducted experiments with these barnacles: he moved rocks housing *Chthalamus* to lower areas and those housing *Semibalanus* to higher areas, and he physically removed *Semibalanus* from rocks in the lower areas and *Chthalamus* from rocks in the higher areas. Connell found that *Chthalamus* was able to survive normally in the lower level on the rocks he had placed there. However, *Semibalanus* did not fare well on rocks in the higher zone, as this species is less tolerant of drying out. It is interesting that Connell also took photographs of larvae of both species equally colonising the lower zone. However, as *Semibalanus* individuals grow, their base expands more rapidly and they literally expel the *Chthalamus* larvae from the rocks. On the one hand, ecological factors influence the vertical distribution of these species; on the other hand, during colonisation of rocks, the acting factor is competition.

Competition can be so intense that one species completely expels another from a habitat. This is known as competitive exclusion. Many allochthonous (alien) species can also expel autochthonous (indigenous) species through this process of competitive exclusion. In many clean rivers that remain in a relatively natural state, the introduction of rainbow trout (*Oncorhynchus mykiss*) has resulted in significant reductions in populations of the native brown trout (*Salmo trutta*). The introduction of alien and invasive species has particularly affected the Dinaric karst rivers of the Adriatic basin, which are rich in endemic species [8]. Another example is the introduction of the American grey squirrel (*Sciurus carolinensis*) in Great Britain between 1876 and 1915 or later. By the mid-1920s, the population of the native red squirrel (*Sciurus vulgaris*) had declined drastically due to disease. The spread of the introduced species co-occurred with the decline of the indigenous species. It has been confirmed that the grey squirrel spread into habitats not inhabited by the native red squirrel, as well as into areas where the native squirrel population was declining due to disease. The introduced species was more competitive for food and habitat, and also more resistant to disease, and therefore displaced the native species in a great part of Britain. The native red squirrel has maintained large populations only in certain isolated localities that were not exposed to the epidemic (e. g. on the Isle of Wight off the south-east coast of Great Britain) [9].

There are countless examples of competition. However, most species with similar needs often share the same habitat. This is considered coexistence, indicating that they have succeeded in overcoming or reducing competition between them. One way different species use a resource is by using it at different times. In forests, predatory bird species such as falcons and buzzards hunt by day, while owls hunt by night. Both groups feed on small mammals. The macrozooplankton of Visovac Lake in Krka National Park (Croatia) consists of four species of water fleas. Of these, two species are in direct competition for food, and both belong to the same order of water fleas (*Daphnia*) [10]. The species *Daphnia longispina* is small and feeds primarily on algae 15–20 µm in size. The second water flea species, *Daphnia cucullata*, feeds on green algae of the same size. However, unlike the first species, this species can also feed on slightly larger amounts of small organic particles. The annual cycle of these two crustacean species is shown in Figure 2.4.

In this case, the spatial and temporal distribution of these species is primarily determined by food sources. *D. cucullata* develops its densest populations in June, when *D. longispina* is not yet present in the macrozooplankton. *D. longispina* begins to appear in July and, as it does, gradually displaces *D. cucullata*. During July, their populations are spatially separated: *D. cucullata* is found at depths of 10 and 20 m, while *D. longispina* occurs at depths of 5 and 15 m. For the remainder of the year, only *D. longispina* is present in the macrozooplankton.

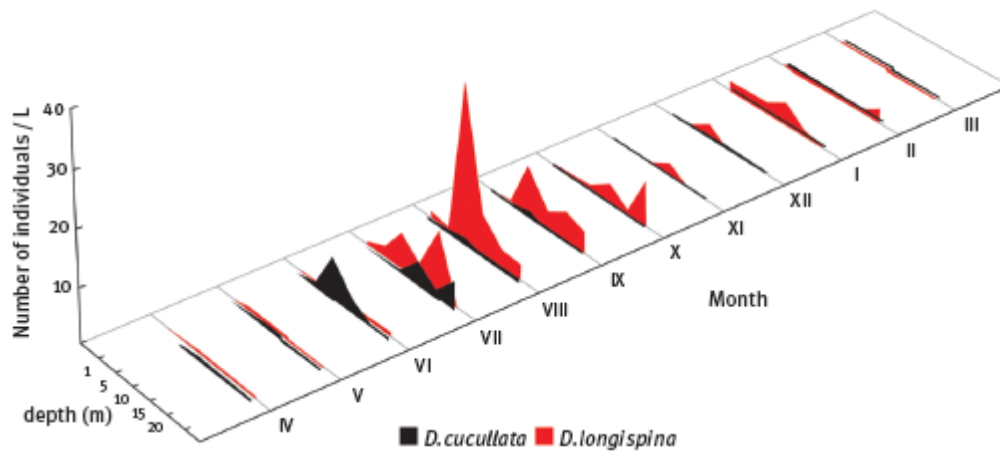


Figure 2.4: Niche separation in space and time between two *Daphnia* species in Visovac Lake.

As shown in these examples, different species can coexist by separating their ecological niches, either spatially or temporally. Most often, the term ecological niche refers to the position of a species in the community in terms of food, which can be considered its microhabitat. The habitat of a species can be described as its “address,” while its niche is its “profession”! Thus, species living at the same “address” do not necessarily have the same “profession.” However, this understanding of the ecological niche has gradually evolved over the past 30 years. Today, many biologists believe that the ecological niche is determined not only by feeding methods, but also by all other ecological factors to which a species has adapted.

There is another way to avoid competition. In Asia Minor, the distribution ranges of two passerine bird species overlap: the western rock nuthatch (*Sitta neumayer*) and the eastern rock nuthatch (*Sitta tephronata*). Both species feed on insects in the soil. The beak size of each species determines the size of prey it can catch. Both nuthatches have a beak 26 mm in length, so it could be assumed that they would feed on insects of the same size and be in direct competition with each other. However, this is not the case in nature. In areas where their distribution ranges overlap, the western rock nuthatch develops a beak 24 mm in length, while the beak of the eastern rock nuthatch grows to 29 mm! In areas where they do not overlap, and are not in competition, both species have a beak 26 mm in length [11]. This phenomenon is called character displacement. It is observed in the fact that species coming into competition in overlapping range areas will change those characteristics that create the competition between them.

Is there competition among plants? Plants address potential competitors through allelopathy, a phenomenon in which certain plants secrete chemical compounds into the soil to inhibit the growth of other plants. For example, walnut or sage releases compounds into the soil that can suppress the growth of other plant species within a radius of several metres.

Predation

Another important biotic factor that can influence the distribution of a species is predation. This is a relationship in which one organism, the predator, consumes another, the prey. The prey is alive when the predator first attacks! Predators can overhunt and completely eliminate prey species from an area, or they can prevent the range expansion and colonisation of new areas by potential prey. Although there is theoretical support for this possibility, there is no actual evidence that it occurs in nature. Such extreme events are only known to occur in cases where species that are not native to an area are introduced.

The influence of a predator on the prey population is clearly detrimental. However, predator effects on a prey population are not always easily predictable. There are two reasons for this. First, prey individuals that are killed or injured do not always correspond to a random pattern of the entire prey population. Predators tend to select prey that are easiest to catch: the young (and naïve), the old (and weak) and the sick (and helpless). Second, predation can affect the growth, survival and reproduction of prey. In other words, while predation is harmful to the prey individuals that are captured and consumed, it can be beneficial to those that are not captured. The case of the Kaibab deer is well known [12]. The initial population of 4,000 of these animals on the Kaibab Plateau, located in northern Arizona in the United States along the northern border of the Grand Canyon, grew to 100,000 in just 20 years (1905–1924) as humans hunted and eliminated their natural predators (the cougar and coyotes), Figure 2.5. This rapid population growth led to intense competition, primarily for food resources, and within the next 15 years, the population declined to 10,000 individuals. Therefore, it can be concluded that the relationship between predator and prey maintains the natural balance!

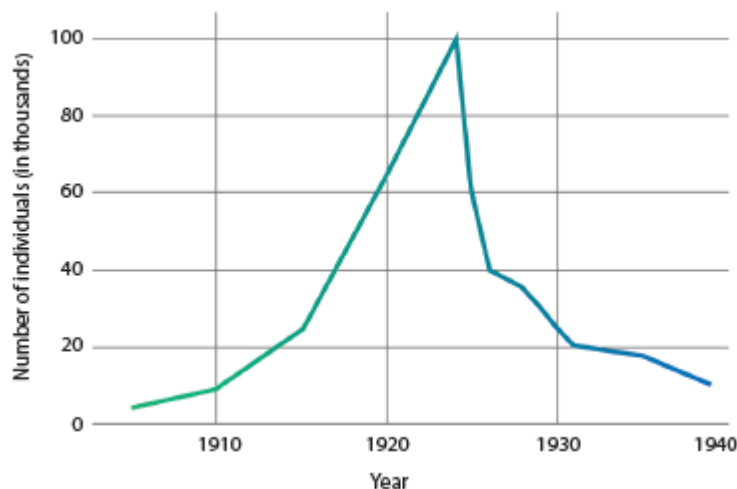


Figure 2.5: Changes in the abundance of Kaibab deer after elimination of natural predators [inspired by www.biologycorner.com/worksheets/kaibab_key.html, Keeton Biological science].

It is also important to identify which prey individuals are affected by predators and at which life stage. Young individuals cannot yet contribute reproductively to the population; therefore, the effects of predation on this segment of the prey population are less significant than if the predator catches a reproductively mature individual. The impact of a predator on prey is not constant but is instead limited to certain periods. For example, the boa constrictor (*Boa constrictor*) rests for a while after eating its prey while it digests. The success rate of hunting prey is not always 100 %, as prey may escape. Additionally, some predators require time to learn how to hunt, and their efficacy changes with age: young tigers or lions are less experienced and effective than adult individuals.

Parasitism

Parasitism is a relationship similar to predation. Parasitism can be considered a special form of predation, in which the predator is usually much smaller than its prey (the host). Unlike classical predators, the parasite typically does not kill its prey. In this relationship the parasite benefits, while the host usually suffers some degree of harm. As with predation, parasites help regulate the natural balance by maintaining host populations at certain levels, ensuring they do not exhaust their food source. However, introduced parasites can cause significant changes in the distribution of potential host populations. Lake trout (*Salvelinus namaycush*) is a widely distributed species throughout northern North America, but it is not adapted to the presence of parasitic lampreys (*Petromyzon* and *Entosphenus*). These lampreys attach to fish and feed on their tissue and bodily fluids. Niagara Falls is a natural barrier that prevents these parasites from entering the Great Lakes, where large populations of lake trout once thrived. However, with the construction of the Welland Canal, which connects Lakes Ontario and Erie, the lampreys spread throughout all the Great Lakes and caused substantial declines in lake trout populations [13].

A similar effect was observed after the introduction of the parasite that causes malaria in birds (*Plasmodium*) to the Hawaiian Islands. The endemic bird fauna of these islands experienced significant population declines in some species, range contractions and even extinctions [14].

Mutualism

Mutualism is a relationship in which both species benefit. This relationship can involve close physical interaction between members. Typically, one member of such a pair becomes completely dependent on the other, making this mutualism obligatory for that species. In extreme cases, these organisms begin to function as a single individual, as seen in fungi and algae in lichens. An example of obligate mutualism is the relationship between protozoans and bacteria in the digestive tracts of certain animals, such as ruminants or termites. Protozoans in the digestive tract of termites break down wood into compounds the host can further digest. Neither organism would be able to survive independently. Mycorrhiza is another form of mutualism. This is a symbiosis between the roots of a vascular plant (such as a tree) and fungi. The fungi supply the tree with nutrients, while the plant provides the fungi with carbon. However, mutualism may also be facultative (not obligatory), in which case mutualists can survive without one another. The most common

example of this form of mutualism is the relationship between hermit crabs and certain sessile anemones. The hermit crab occupies an empty snail shell, on which one or more anemones can settle. The anemones defend the crab with their stinging cells, and as sessile organisms, the crab serves as their “means of transport.” However, both organisms can survive without the other.

A special form of mutualism is also evident in the relationship between certain plants and insects or birds as pollinators. Coevolution has progressed significantly in this context, as seen in the shapes of flowers, their colouration, and the specialised mechanisms developed by plants and their pollinators. Some of the most unusual examples of mutualism are found in the relationship between ants and certain plants. South American acacia species (*Acacia*) have thorns in which some ant species of the genus *Pseudomyrmex* build their nests [15]. The plant produces protein-rich Beltian bodies (which resemble berries) and sweet fluids that the ants feed on. In return, the ants protect the plant from attack by

other herbivorous insects and vertebrates. They also eliminate surrounding vegetation, reducing competition with other plants. This specialisation has resulted in identical distribution ranges for these two species.

Commensalism

Commensalism is a relationship in which one species benefits while the other is neither helped nor harmed. The Adriatic Sea is home to small, soft-bodied crabs of the family Pinnotheridae, which have commensal relationships with numerous bivalves, ascidians and the tubes of polychaete worms (Polychaeta). Among the many genera and species, the most common are the crabs that inhabit the noble pen shell and those that inhabit oyster and mussel shells. The bivalves are not disturbed by these small crabs, which seek shelter from predators. Another example of commensalism is epiphytic plants. These are mostly tropical plants that live on the branches of other plants. They use only the space where organic material and water have collected, and have no other impact on the host plant.

2.2.3 Community

No organism in nature lives in complete isolation. A collection of organisms interacting directly or indirectly within a habitat forms a community. The concept of a community originated from botanists' efforts to group certain plant formations. In the early twentieth century, American scientist Frederic Clements [16] proposed that plant units, which he called “associations,” are strictly determined and remain fixed for long periods. Today, the term “community” refers to all living organisms in the same habitat, among which there are relations of mutual dependence and biological connections. Their interactions are important for the functioning of the community.

2.2.3.1 Community structure

The community is characterised not only by a mixture of species, but also by physical features. On land, the vertical structure of the community is mostly determined by plants. Their height, branching and the amount of leaves determine the vertical gradients of temperature, moisture and light (Figure 2.6). Plants form the framework of the community to which animal species are adapted. A well-developed forest ecosystem contains several layers of vegetation: the canopy layer, the understory, the shrub layer, the ground layer and the forest floor. The canopy plays the most important role in the fixation of solar energy. Aquatic systems, such as lakes and oceans, are also vertically stratified, primarily due to light penetration.

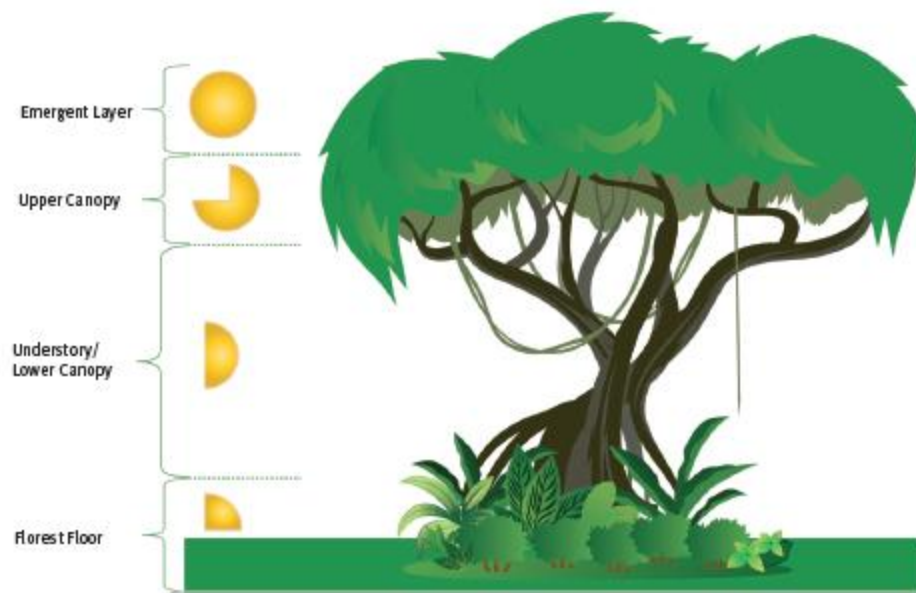


Figure 2.6: Forest vertical structure and vertical light gradient.

The horizontal pattern of communities in space is variable. It usually includes differences due to latitude and altitude. Increasing latitude and altitude result in more extreme conditions, so the composition and appearance of the community change.

2.2.3.2 Community sustainability

In the early twentieth century, two American scientists, Frederic Clements and Henry Gleason, raised the question of community sustainability (equilibria).

Clements [16, 17] developed the “*organism concept of community*.” In this concept, each species in the community represents an interacting component of the whole. The main processes shaping the community are mutualism and coevolution (predator–prey or competition interactions). In contrast, Gleason [18, 19] supported “*the individualistic continuum concept*.” The community very rarely, if ever, reaches a state of equilibrium.

Communities, therefore, are not highly regulated species groups, but rather random populations of plants and animals, in which each individual responds specifically to changes in the environment. Biological factors such as competition and predation have no significant impact on community sustainability or equilibrium.

Many studies have been conducted over the past 50 years to support one of these theories. Some have shown that predation and competition play important roles in regulating the community. Rapid changes in the physical environment can strongly affect the composition and structure of the community. Climate change, weather, and natural disasters can also significantly affect communities.

2.2.3.3 Biodiversity

Biological diversity (biodiversity) is the variety of life on Earth. It includes genetic, ecosystem, and species variation [20] within an area, biome or the entire planet.

Diversity is estimated on the basis of species richness (the number of species) and species abundance (the number of individuals per species). To estimate biodiversity, many indices are used; the most common is the Shannon-Wiener index:

$$H = - \sum_{i=1}^S (p_i)(\log_2 p_i)$$

where H is a diversity of species, S is the number of species, and p_i is the proportion of individuals in the total sample belonging to the i th species.

The number of species is changing over time (Figure 2.7). The fluctuations in diversity and extinction rates result from changes in various biotic and abiotic factors. Climate change is believed to have the greatest impact [21]. Human activities disrupt the natural balance, causing the extinction of many organisms, especially in the last century.

2.2.4 Ecosystem

The concept of a community includes only living organisms in a habitat but ignores the physical environment, such as nutrients and energy that enable the survival of living organisms. An ecosystem is a spatial or organisational unit comprising organisms and their physical environment. The environment consists of biotic and abiotic components linked through nutrient cycles and energy flow. Simply put, all ecosystems (terrestrial and aquatic) have three important parts: producers, consumers and the non-living environment (Figure 2.8).

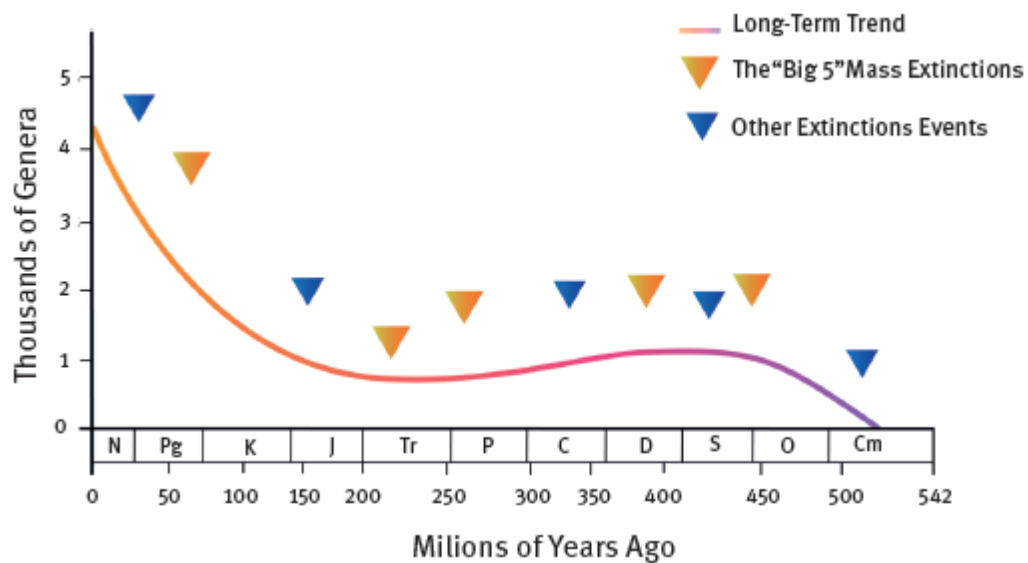


Figure 2.7: Apparent marine fossil diversity during the Phanerozoic; N – Neogene, P – Paleogene, K – Cretaceous, J – Jurassic, Tr – Triassic, P – Permian, C – Carboniferous, D – Devonian S – Silurian, O – Ordovician, Cm – Cambrian, inspired by [22].

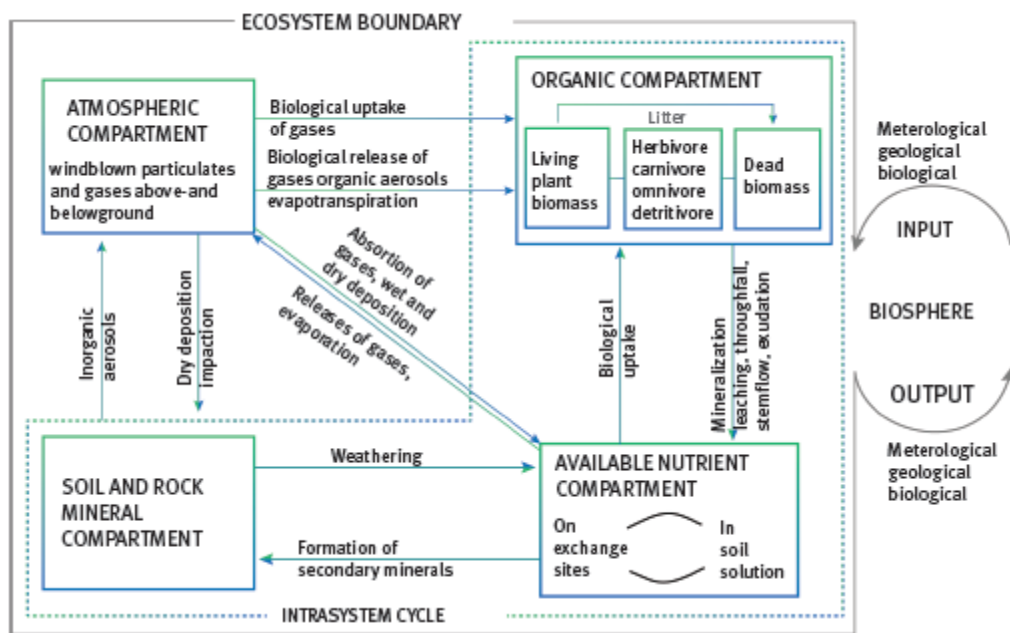


Figure 2.8: Schematic representation of the ecosystem; inspired by [23].

The energy that flows through ecosystems is obtained primarily from the sun. It generally enters the system through photosynthesis. The energy accumulated in this process is called primary production. Total annual primary production on Earth is 162.41

$\times 10^9$ t. Approximately one third of it occurs in the sea with the remainder on land. Among the most productive ecosystems in the world are wetlands; however, their contribution to global production is small because they cover only a very small part of the Earth's surface.

In terrestrial systems, production is determined by temperature and precipitation, as these directly affect the level of photosynthesis. In the oceans, production is limited by light penetration. Phytoplankton (and plants) are located mainly in the surface layers of aquatic ecosystems, where there is sufficient light. However, primary production also depends on the availability of nutrients, which must be transported from deeper parts to the surface layers.

The energy stored in plants moves through the ecosystem in a series of steps called food chains. A food chain shows how organisms are related to each other by the food they consume. Each level of a food chain represents a different trophic level, starting with producer organisms (plants) and ending with apex predator species (carnivore). One type of plant can be a food source for many herbivores, but many carnivores can hunt the same prey. Therefore, in the ecosystem, many food chains are interconnected in food webs.

Organisms in the food chain can be grouped into trophic levels according to the type of food they consume. In general, all organisms that feed on other organisms are called consumers or secondary producers. Consumers can be divided into subgroups, each representing a single trophic level: those that feed on plants (primary producers) are called herbivores or primary consumers. Carnivores (meat-eaters) or predators feed on herbivores (plant-eaters) are called secondary consumers. Almost every habitat, including freshwater ecosystems, contains consumers who do not fit entirely into the simple scheme of trophic levels. These consumers – decomposers or detritivores feed on the dead remains of other organisms (detritus). Their role may not seem important at first glance, but they are a crucial link in the flow of energy and nutrient cycling within the ecosystem. Decomposers are involved in breaking down of dead plants and animals, returning nutrients to the cycle and thus enabling the growth and development of primary producers.

The amount of energy transferred from one trophic level to another is very difficult to determine. When summed, the biomass, or energy at each trophic level forms an ecological pyramid. This is also called Elton's pyramid, according to Elton [24]. In general, the biomass and energy of producers must be greater than those of secondary producer: the base of the pyramid determines the size of each subsequent trophic level (Figure 2.9).

According to the second law of thermodynamics, as energy transfers between different trophic levels, some is lost as a heat, which limits the number of links in the chain. Highly productive systems do not support long food chains; however, they contain many species, resulting in a very complex web. Ecosystems subject to rapid changes in abiotic factors have shorter food chains compared to more stable ones. Highly stratified systems, such as forests or pelagic ocean food chains, are longer than less stratified systems, such as meadows, tundra or benthal of a stream.

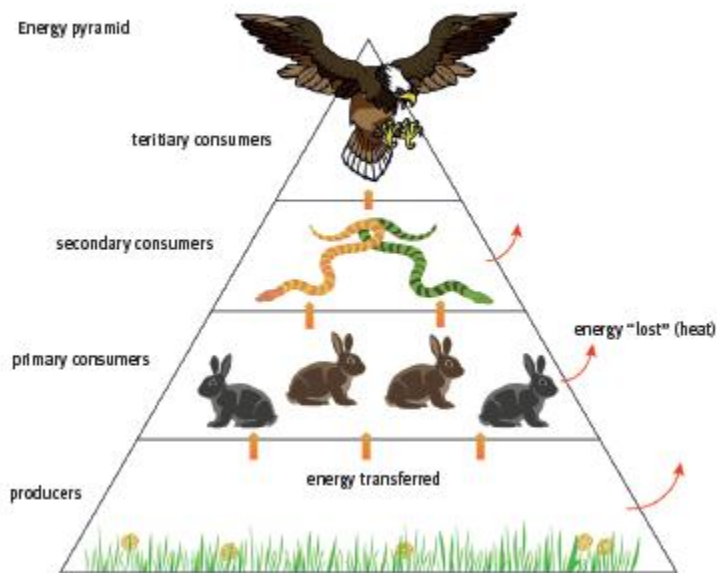


Figure 2.9: Energy pyramid.

2.2.4.1 Biogeochemical cycles

All nutrients are transported through the ecosystem from non-living to living components in cyclic paths called biogeochemical cycles. The most important biogenic elements such as carbon, nitrogen (Figure 2.10(a)), phosphorus, and sulphur are incorporated into living organisms within food chains and, through the decomposition of dead organisms, are returned to the lithosphere. The entire cycle then begins again. The main driver of these cycles is solar energy and the water cycle plays a particularly important role for all biogenic elements (Figure 2.10(b)).

Carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur make up 95 % of the biomass on Earth and are called macroelements. Macroelements, together with calcium, silicon, magnesium, sodium, potassium, chlorine and iron (microelements) constitute 99 % of the dry weight of living organisms. Other biogenic elements, such as manganese, molybdenum, copper, vanadium, and nickel, occur in much lower concentrations as trace elements.

2.2.4.2 Ecosystem biodiversity and stability

One of the basic questions in ecology is: how many species are necessary for the normal functioning of an ecosystem? Is there a minimum number, or are there redundant species in the system? If there are redundant species, which species are necessary for the maintenance of the ecosystem?

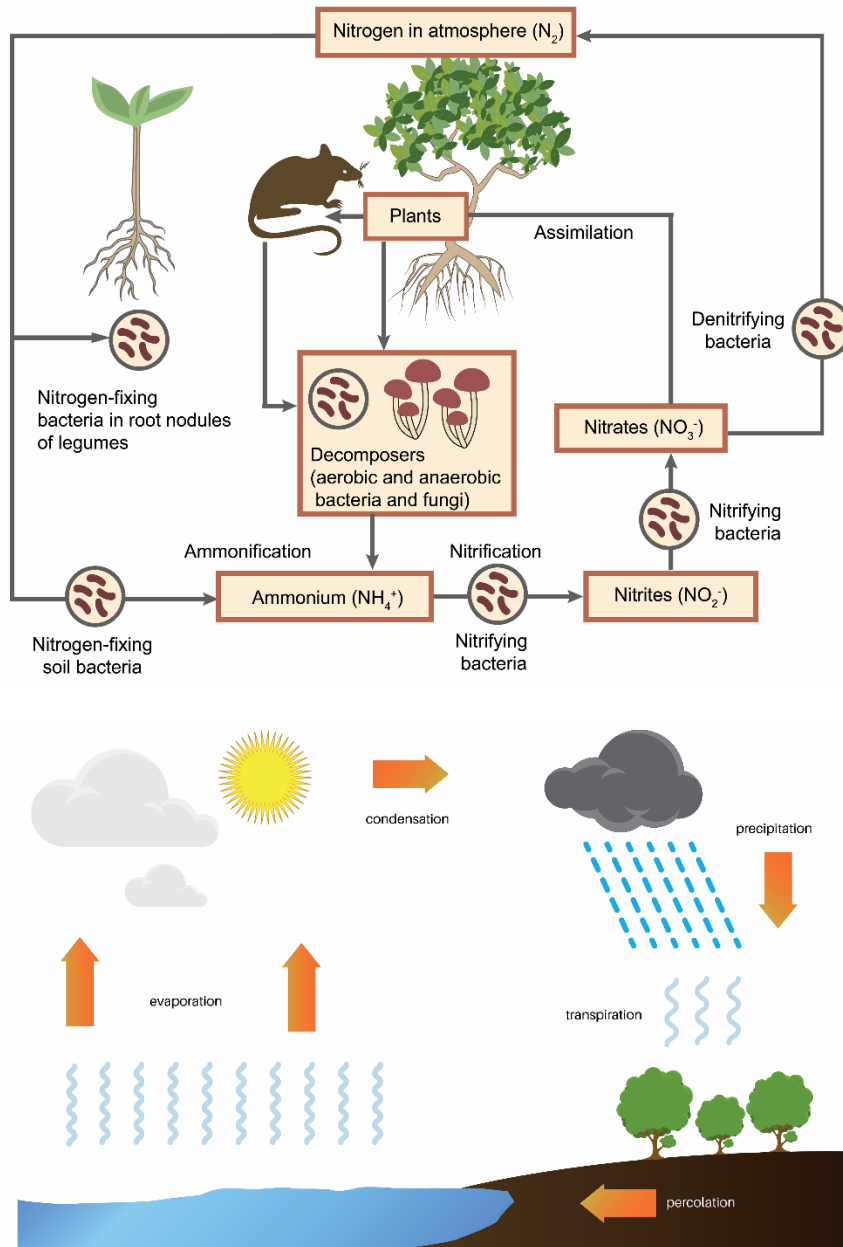


Figure 2.10: (a) nitrogen cycle (b) water cycle..

If we assume that all species are essential for the functioning of the ecosystem, then the loss of any species causes imbalance, leading to degradation or collapse of the whole system (Figure 2.11). Alternatively, if species diversity in the ecosystem has no influence on its function, the loss of any species may cause random and unpredictable consequences.

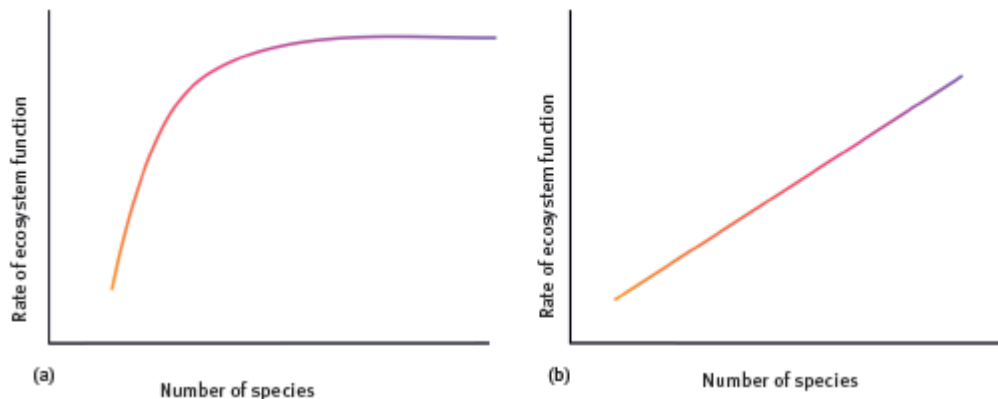


Figure 2.11: The potential relationship between the number of species in an ecosystem and its functioning (primary production, decomposition, circulation of materials): (a) redundant species hypothesis; (b) dependent species hypothesis [25].

These models were tested both in the laboratory and *in situ*. The first laboratory research on this subject was conducted by John Lawton with a group of researchers at Imperial College London [26]. They found that ecosystems with a large number of species have more efficient primary production, develop a more complex plant cover and accumulate more nutrients. Their results support the second hypothesis: that a reduction in biodiversity leads to poorer ecosystem functioning. However, it is possible that the further addition of species to a system leads to a saturation point, so this experiment does not fully answer the question posed at the outset. In any case, this research demonstrates that the third hypothesis can be rejected: ecosystem functioning is not random in relation to biodiversity.

The group of authors from the University of Minnesota conducted similar studies [27]. Their results were similar to Lawton's research: greater biodiversity leads to a better ecosystem functioning. However, they found that not all species in the system are equally valuable. The value indicates how much the loss of a particular species impacts the entire ecosystem, but also that some species depend on each other. For example, plants belonging to the legume family (Fabaceae) are very important for nutrient cycling in the ecosystem, as their roots have symbiotic bacteria that can bind elemental nitrogen. The circulation of nitrogen is one of the basic biogenic cycles important for all organisms. By fixing nitrogen, these plants provide more nutrients in the soil, which in turn results in greater production of other plants and animals connected to them in the food chain. Therefore, the loss of legume species can have a major impact on the productivity of the entire system. These species are often called "keystone species," because of their importance to the functioning of a system.

Another issue of extraordinary importance regarding biodiversity and ecosystem function is whether biodiversity influences ecosystem stability.

British ecologist Charles Elton observed in the 1950s that more complex and richer systems are less susceptible to sudden changes. However, the development of mathematical modelling and the use of simulation in population ecology did not produce the same results. Models showed that the populations of some species, even in diverse ecosystems, are subject to fluctuations caused by external factors such as disease or drought. It is possible that, regardless of variations in individual species, the functioning of the entire ecosystem remains unchanged. Thus, the population of a certain species may fall or rise, but the ecosystem survives because many other populations continue to maintain the system's function.

2.2.5 Succession

Communities in an ecosystem change over time. These changes are called succession. More accurately, succession refers to a series of changes in communities within a certain period. Succession occurs in both terrestrial and aquatic systems. We distinguish between primary and secondary succession. Primary succession takes place on previously completely bare surfaces (without life). Secondary succession occurs in already populated habitats after a disturbance.

On 28 August 1883, at 10:02 pm, an extraordinary disaster occurred. The Indonesian island of Krakatoa exploded in one of the largest volcanic eruptions in recent history. Most of the island was destroyed in the explosion. At the site of the former island of Krakatau, two smaller islets were formed: Anak Krakatau and Rakata. The island of Rakata was completely sterilised, and all life on it was destroyed. The first expedition arrived at Rakata eight months after the explosion and found only one living creature on the island: a single spider! Scientists continue to study the colonization of animals and plants on this completely bare area. After three years, the first living organisms were observed on the island: blue-green algae inhabited areas of cooled volcanic ash. Mosses soon followed; they are the pioneer species, the first colonists of a habitat.

Pioneer species formed the foundation for the settlement of other organisms. After 25 years, the tropical forest developed, bringing with it characteristic fauna such as birds, snails, butterflies, bats, and others. In 1983, scientists recorded a total of 420 taxa on Rakata Island (Figure 2.12). During the colonisation of Rakata, several communities succeeded one another. In succession, plants always preceded animals, creating a habitat for them.

2.2.5.1 Climax

According to classical ecological theory, succession ends when of late-successional species become dominant. At this stage, the community is stable, and disturbances cannot significantly alter the system. This final stage of succession is called the climax.

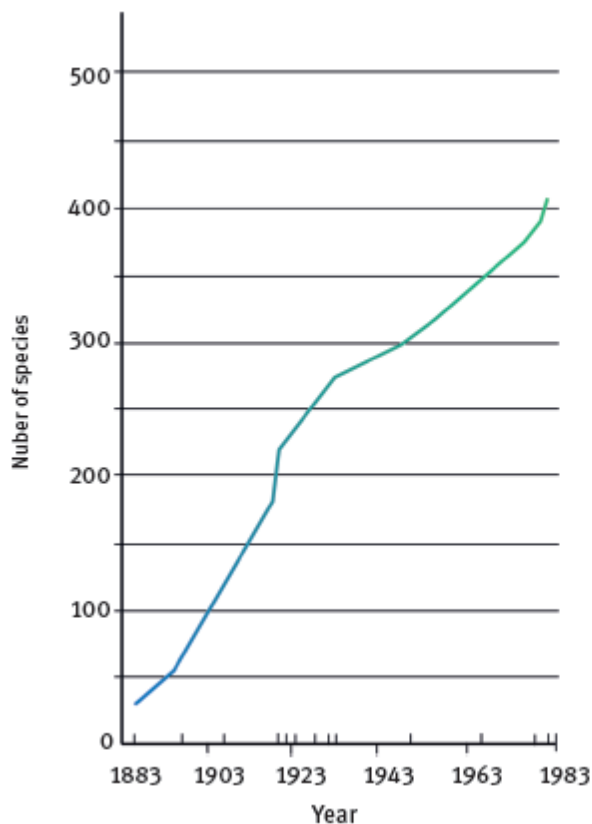


Figure 2.12: The number of species on Rakata Island over time after the Krakatau Island explosion; inspired by [28].

Community climax theoretically has certain characteristics: the community achieves a balance between total primary production and total respiration; energy is obtained from sunlight and decomposition; there is a balance between the nutrient consumption and nutrients returned through decomposition. Each individual in the climax stage is replaced after death by another individual of the same species; species composition is in a state of equilibrium.

Many communities that appear balanced actually undergo successive changes much more frequently than we realise. Tropical forests in Central America are frequently exposed to natural disasters. Tropical storms and hurricanes occur very often in this region and have a significant impact on the communities. According to some estimates, tropical storms affect the same area (community) every 60 years, leaving behind devastation such as broken trees or full or partial defoliation of vegetation. The destruction of vegetation cover, of course, affects wildlife, also causing changes in the composition and distribution of animal habitats. Therefore, climax should be considered a dynamic equilibrium of the community. Even an “old” and apparently stable community is constantly undergoing dynamic change.

2.2.6 Biomes

Climate largely determines plant formations and the life within them. These formations are called biomes. There are several major terrestrial biomes: tundra, grassland, desert, taiga, temperate forest, Mediterranean vegetation, and tropical rainforest. They are further divided into types depending on climate and altitude (Figure 2.13).

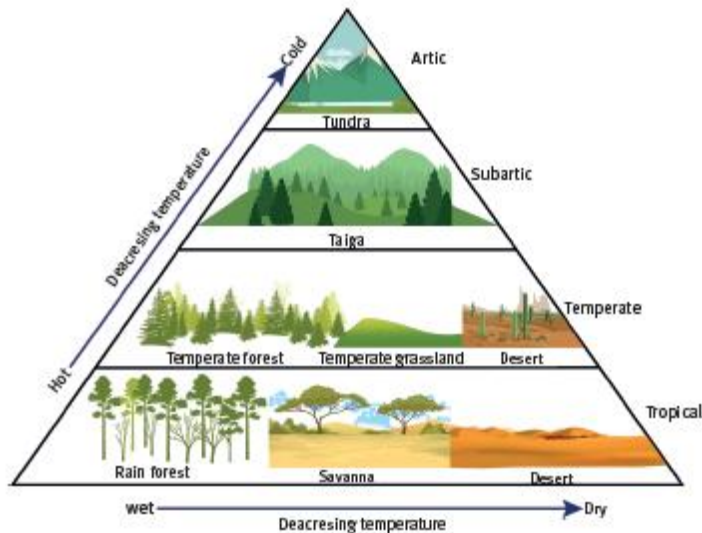


Figure 2.13: Biomes; inspired by [29].

Although inland waters (freshwaters) accounts for just over 0.5 % of all water on Earth, their importance is considerable. They are used for drinking, industry, and agriculture. Inland waters include groundwater and surface water. Surface waters comprise running waters such as rivers and streams, and standing waters such as pools, ponds, and lakes.

Seas and oceans cover more than 70 % of the Earth's surface and are inhabited by living organisms from the surface to the bottom. The chemical composition of seawater is very stable; more than 85 % of the total amount consists of NaCl. Temperature fluctuations in the surface layer depend on geographical location. In addition to temperature, pressure has a significant impact on life in the sea, increasing with depth. Deep layers have a constant temperature, while in the surface layers (up to 200 m) temperature varies. There are two main habitats in the sea: the bottom and the water column. The sea bottom is a very diverse habitat and is inhabited by benthic organisms. Plankton and nekton organisms live in the water column.

2.2.7 Global changes

Today, human activities cause environmental changes that disrupt the normal functioning of the biosphere. Major changes include global warming, ozone depletion, acid rain and habitat destruction.

2.2.7.1 Greenhouse effect

In the past 100 years, the concentration of CO₂ in the atmosphere has increased by about 25 %, mainly due to greater exploitation and use of fossil fuels. Excessive amounts of CO₂ in the Earth's atmosphere are intensifying the greenhouse effect. The Earth's surface absorbs solar radiation and then emits it as longwave radiation or thermal energy. CO₂ traps this longwave radiation, thereby heating the Earth's atmosphere. This process is called the greenhouse effect and leads to global warming. According to some predictions, by the year 2100, the average temperature on Earth will increase by between 2 °C and 4.8 °C. The consequences include climate change, which may cause drastic changes in the distribution of individual plant and animal species, leading to problems in food production and the transmission of various diseases (malaria, influenza and yellow fever).

2.2.7.2 Acid rains

Precipitation such as rain and snow is naturally slightly acidic, with a pH between 5 and 5.6, due to the presence of carbon dioxide (CO₂) in the air. Acid rain refers to any precipitation with a pH lower than 5. Such acidic precipitation is caused by increased levels of various air pollutants, particularly sulphur dioxide (SO₂) and nitrogen oxides (NO_x). Precipitation with low pH damages plants, causes acidification of lakes and rivers and directly affects the organisms living in them. Acid rain may also lead to soil acidification. As a consequence, heavy metals leach into terrestrial and aquatic ecosystems. Heavy metals are toxic to living organisms; in vertebrates, they accumulate in the liver and brain and can cause serious damage to these organs.

2.2.7.3 Ozone depletion

Ozone, O₃, is a form of elemental oxygen that is important for absorbing of ultraviolet radiation in the stratosphere. It absorbs 97 % to 99 % of UV radiation which can cause severe damage to DNA. Depletion of the ozone layer can be caused by freons (various halocarbon products typically used as refrigerants and aerosol propellants), the detonation of nuclear weapons, and exhaust gases over large urban centres.

2.2.7.4 Habitat fragmentation

At the beginning of this chapter, we emphasised that human impact on nature is significant. One global environmental problem is the destruction of habitats. The construction of roads, railways, power lines, the expansion of settlements and agricultural land use have caused the destruction and fragmentation of natural habitats. Such fragments of natural habitat are often insufficient to maintain populations. One major problem of habitat destruction is deforestation, particularly in the tropics. In addition to the degradation of forest communities, it also causes drastic climate change.

2.2.8 Applied ecology

2.2.8.1 Constructed wetlands

Constructed wetlands are treatment systems designed to improve water quality. They use natural processes involving wetland vegetation, soils and associated microbial assemblages to treat anthropogenic discharges such as municipal or industrial wastewater or stormwater runoff.

Constructed wetlands can be designed to emulate the features of natural wetlands, such as functioning as biofilters to remove sediments and pollutants from water. Some constructed wetlands may also provide a habitat for native and migratory wildlife, although this is usually not their primary purpose.

Vegetation in a constructed wetland provides a substrate (roots, stems, and leaves) for microorganisms to grow as they break down organic materials (Figure 2.14 and Figure 2.15). The plants remove about 7–10% of pollutants and serve as a carbon source for the microbes which are responsible for approximately 90 % of pollutant removal.

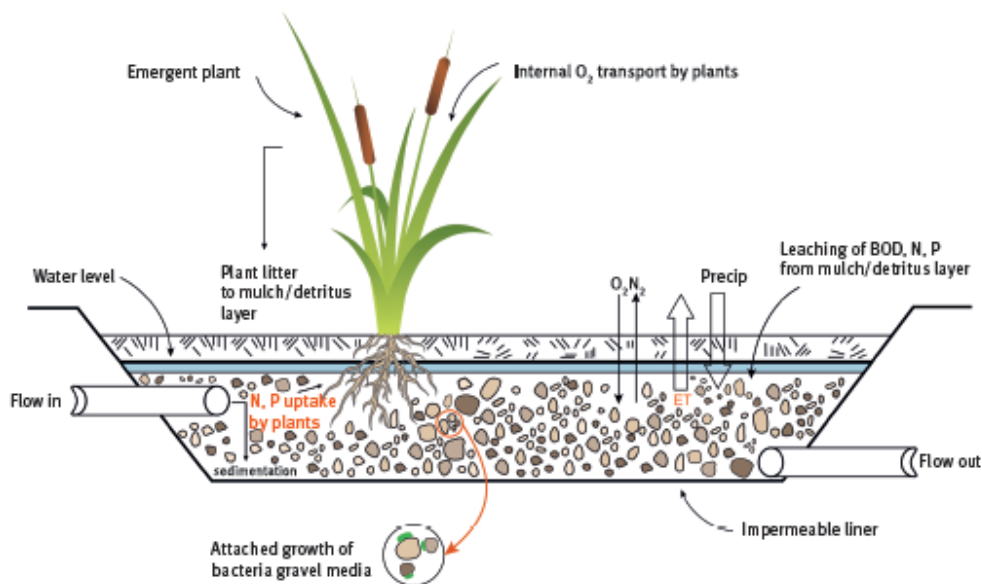


Figure 2.14: Constructed wetland; inspired by [30].



Figure 2.15: Constructed wetland in location Hrušćica near Zagreb; photo by Renata Horvat.

2.2.8.2 Water framework directive

Freshwater ecosystems are among the most degraded on the planet. Numerous human activities impact water quality, including agriculture, industry, urbanisation, disposal of human waste, mining and climate change. In 2000, the European Union established its framework for the protection, improvement and sustainable use of Europe's water resources by launching the Water Framework Directive (WFD) [31]. The WFD is considered pioneering because it prioritises the ecosystem approach, that is, the integrated consideration of chemical and ecological status in defining water quality [32]. The overall status of surface waters is determined by whichever of the two is worse. The chemical status of surface waters is assessed using a list of priority substances (complex organic compounds) and other pollutants. The European Commission establishes and periodically revises the list of priority substances (and priority hazardous substances) that pose a significant risk to the aquatic environment. The priority substances most frequently found in the surface waters of EU Member States at levels exceeding prescribed environmental quality standards are mercury and polybrominated diphenyl ethers. Ecological status parameters are presented in Table 1. The overall ecological status is determined by the quality element with the poorest status.

Measuring ecological status enables the evaluation of the effects of human activity on water ecosystems and serves as an essential tool for the sustainable management of water resources. Legislation requires the periodic assessment of all water bodies, including rivers, lakes, estuaries, coastal waters and groundwaters. The first and fundamental step in implementing the WFD for surface waters is their typification, allowing a type-specific approach to water quality assessment [33]. Water types are then assigned to a classification system that grades their deviation from the reference state (high, good, moderate, poor and bad), with no or only very minor disturbance from human activities. In Croatia, 19 river

types have been identified. The WFD requires EU Member States to develop classification systems to describe the ecological status of a given water body. Pozojević et al. [34] developed an ecological status classification system for Croatian lakes. The main objective of the WFD is to implement measures to achieve “good ecological status” for all natural water bodies. The emphasis placed by the WFD on ecological elements has been widely welcomed by scientists and environmental managers, as it focuses risk management efforts on restoring those impacted ecosystems classified as being of less than “good ecological status.”

Table 2.1: Ecological status quality elements of surface waters according to the Water Framework Directive.

Ecological status quality element	
Biological	Phytoplankton
	Macrophytes
	Phytobenthos
	Benthic macroinvertebrates
	Fish
Hydromorphological	Hydrological Regime
	River Continuity
	Morphological Conditions
Physico-chemical	Thermal Conditions
	Oxygenation Conditions
	Acidification
	Nutrients
Specific Pollutants	National/river basin specific synthetic and non-synthetic pollutants

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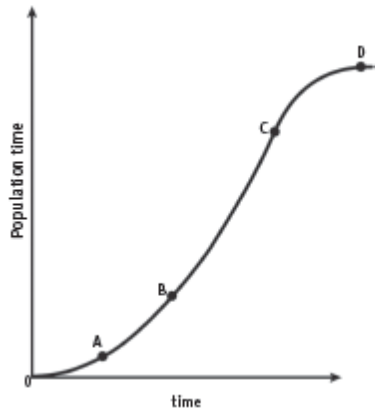
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Study questions

1. What do several different populations living together form?
A) a biosphere; B) an organism; C) a community; D) an ecosystem
2. When there is significant pollution, rain can become acidic, harming plants and animals. What is this an example of?
A) competition between a population and a community; B) a mutualistic type of symbiosis; C) an abiotic factor affecting an ecosystem; D) an individual affecting a community
3. Bears eat fruits such as berries and animals such as fish. They hibernate in winter. Which of these terms applies to bears?
A) they have a mutualistic relationship with berries; B) they are at the bottom of the energy pyramid; C) they are decomposers; D) they are consumers.



4. The carrying capacity of the environment, for the population shown in the diagram is best represented by a point on the curve marked with a letter:

A) A; B) B; C) C; D) D.

Table 1: Population density.

Level	Population
1	53
2	361
3	823
4	6283

5. In a simple ecosystem, a census of the populations in four successive trophic levels was taken as shown in Table 1. If Level 1 is composed of photosynthetic autotrophs, then the trophic level with 823 individuals will most likely represent:

A) primary consumers; B) secondary consumers; C) decomposers; D) producers.

6. What effect does biodiversity have on a community?

A) it makes destruction by insects impossible; B) it makes primary succession more likely; C) it enables species to survive in a desert; D) it enables the community to withstand changes.

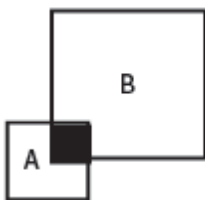
7. Precipitation and evaporation are important components of the

A) nitrogen cycle; B) water cycle; C) carbon cycle; D) phosphorus cycle.

8. Match each item with the correct statement:

A) the populations in an ecosystem 1) food web

- B) made up of interconnected food chains 2) abiotic
- C) the model that shows feeding relationships 3) food chain
- D) living things in an ecosystem 4) biotic
- E) non-living things in an ecosystem 5) community
9. A certain area in north-west Europe (peatlands) stores 30 million tonnes of carbon. In pristine condition, these peatlands can store an additional 15,000 tonnes of carbon per year.
- A) Given this rate of productivity, how long would it take for the peatlands to sequester this amount of carbon?
- B) One prediction of climate change models is a reduction in rainfall in this part of Europe. This would transform the peatlands into a carbon source, emitting up to 462,000 tonnes of carbon per year. How many years would it take to respire all the carbon stored in the peatland?
- C) What is the effective residence time of the carbon that enters long-term storage in the peatland if there is no disturbance in the ecosystem? (Note: this is not a calculation problem!)
10. Base your answer to the following question on the diagram below. A pair of wild goats, A, lives on 1 square kilometre of land. A second pair, B, lives on 4 square kilometres of land, of which 0.25 square kilometres overlap with the territory of the first pair.



Both pairs A and B are members of the same species. Which of the following explains why area B is larger than area A?

- A) Pair B is bigger; B) Pair B has less food in its area; C) Pair A has fewer offspring; D) Pair B has more available resources.

Solutions

1. C; 2. C; 3. D; 4. B; 5. B; 6. D; 7. B; 10. B;

8. A) the populations in an ecosystem 5) community

B) made up of interconnected food chains 1) food web

C) model that shows feeding relationships 3) food chain

D) living things in an ecosystem 4) biotic

E) non-living things in an ecosystem 2) abiotic

9. A) $30,000,000 \text{ tonnes C} / 15,000 \text{ tonnes C yr}^{-1} = 2000 \text{ years}$;

B) $30,000,000 \text{ tonnes C} / 462,000 \text{ tonnes C yr}^{-1} = 64,9 \text{ years}$;

C) Theoretically, infinite: the net community productivity is stored in peat indefinitely.