Dan Cogălniceanu • Biodiversity

Biodiversity

Dan Cogălniceanu

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Foreword

The word *biodiversity*, an abbreviation of *biological diversity*, emerged first as a purely scientific term in the late 1980s, but became the key term of an international environmental law signed at the Rio Earth Summit in 1992.

Biodiversity, defined as “the variety of life on earth, including all genes, species and ecosystems and the ecological processes of which they are part“ has continued to grow as and has become one of the key buzzwords of the 1990s, even making the front cover of National Geographic in February 1999.

But the definition creates a problem for students of biodiversity. How does one become an expert on an estimated 5-10 million species, each comprising diverse populations of maybe billions of individuals, each containing up to 50,000 genes and interacting in ecological communities of maybe 10,000 species per hectare, some of which have persisted for thousands of years and some of which are newly created and rapidly evolving? Anyone claiming to be a biodiversity expert is in danger of being a “jack of all trades, master of none”

Yet it is vitally important for the future health of the planet that we build a generation of biodiversity experts and more importantly, biodiversity advocates, who will study, publish, lobby and campaign for the right of life forms, other than humans, to continue to coexist with us on the planet of their birth.

To study something as broad as biodiversity, it is important to have some kind of “mental map” or framework, within which to position or file so much information. Looking back over 20 years of slowly accumulating knowledge of biodiversity, I now realize how important it is to have some kind of organizational structure to allow one to file and retrieve so many interacting facets of biodiversity information.

There is no single prescription for such a mental map – each of us has to develop our own, specifically suited to our own particular predilections within the totality of biodiversity. No one sees the world, or biodiversity in the same way. For example, to an elephant biologist, dung may be a waste product, or perhaps the only practical way to estimate forest elephant populations. To an insect ecologist, dung is the habitat for a myriad of dung beetles and other insects. To a natural resource manager, the same dung may be a source of sustainable revenue as fertilizer or even for paper-making.

A primer on biodiversity is therefore an important, and useful, entry point in to a fascinating and endless sphere of study – but writing one is a hard challenge, requiring the author to be a total biodiversity expert, able to reduce vast amounts of information to less than 100 pages.

Dr Dan Cogălniceanu has taken on that challenge, summarizing his own personal journey into, and through the biodiversity literature jungle, and cutting a path for the rest of us to follow. If we follow his path, we will not only learn something about most aspects of biodiversity, but also find branching points (references) to enable us to strike out on our own paths into areas which a short primer cannot touch.

The future of biodiversity on this planet depends on us following these paths, recognizing the beauty of biodiversity, and becoming activists for its right to coexist with humanity.

Dr. David Duthie

United Nations Environment Programme, Nairobi, Kenya.

August 2002

Preface

There is an increasingly growing literature on biodiversity and it seems that everything worth mentioning was already done, at least for now. Nevertheless, I will try in this book to carve myself a small niche, focusing on aspects related to species diversity. The concept of biodiversity is too broad in coverage and tends to become empty of content, difficult to perceive and understand by most people. On the other hand, species diversity is clearly defined and I consider it to be the best approach for understanding the major topics related to biodiversity. Although not always referring to it, the ultimate goal is the conservation and sustainable use of the different components of biodiversity. Without this goal in mind everything would be futile.

It is extremely hard to compete with the excellent books already published on the topic, but within the variety of terms, concepts and contradicting views a rearrangement might prove useful. I am myself a newcomer in the field of biodiversity, attracted by a small component of it, amphibians (i.e. frogs, toads, salamanders and newts), that I dedicated most of my work until now. Because of my fondness for amphibians I deserted biochemistry for ecology and conservation and never regretted it, partly due to the fact that I was guided on this new path by several wonderful persons and scientists: Dr. Ion Fuhn, Dr. Doc. Petru Bănărescu and Prof. Dr. Doc. Nicolae Botnariuc. They played a major part in my formation, but should not be held responsible for my mistakes.

The book was written while I lectured at Fachhochschule Eberswalde, at the International Forestry and Ecosystem Management programme, during 2001-2002, on a DAAD grant. I am extremely grateful to the DAAD who provided me with the motivation for embarking on this work. My colleagues and friends in Eberswalde made my stay extremely pleasant and helped me get over the difficult moments. Most of all I am grateful to Michael Mussong, Astrid Schilling, Oskar Dietterlich and Thorsten Mrosek. My students at the University of Bucharest, University Ovidius Constanța and at Fachhochschule Eberswalde provided the motivation needed for persisting in this field.

Many people helped me while writing this book, most of all David Duthie, without whom, the book would be much worse than it is. Dorel Ruşti and Dana Ghioca also provided helpful comments on parts of the book, while Robert Whittaker, Fred Grassle, Manuela Zamfir, Alistair Crame, Alain Dubois, Dan Manoleli, Dorel Ruşti and Benjamin Piña provided some of the needed literature. Danielle Vorreiter checked my English.

I tried in this book to introduce the reader to the concept of biodiversity the way I see and understand it at present. Biodiversity is extremely dynamic in time and space and I expect my own views and opinions to change in time. Nothing is perennial, especially in this field. Rosenzweig (1995) wrote: “Clear writing brings a grave danger. People may begin to understand you! Then they will probably disagree with you.” It is a nice thought that the reader might disagree with me because of my clear writing.

Dan Cogălniceanu

Bucharest, 2007

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1. Biodiversity – an introduction

1.1 Origins of the concept

Our society is facing huge problems at an unprecedented scale: poverty, depletion of vital resources, extensive environmental destruction, emergence of new diseases, wars and famine. These major challenges to our well-being and even survival, despite being apparently unrelated, are all the result of our unfair, unsustainable way of life. History offers many examples of human societies that made major changes to their environment. They had to adapt to the changes they made by altering the patterns of their societies, or disappear. This has happened in every historical period and in every part of the inhabited Earth (Hughes, 2001). At present, we are facing the challenge of adapting on a global scale. A different approach in the way we perceive and exploit the natural resources and the way we share them is required. This adaptive process is extremely complex and needs a radical change in our life-style and beliefs. The Western view of humanity's place in nature is dominated by a dualistic opposition between nature and culture (Haila, 2000). Most religions made us believe that we are a superior species with special privileges (e.g. "So God created man in his own image", Old Testament, Genesis 1:27). Even Darwinism supports the idea that humans are the result of a long process of selection that allowed only the survival of the fittest. These ideas have been most often (mis)interpreted as humans being the most evolved species with special rights and power over the rest of the species inhabiting the planet. We must realize that we are just part of a larger, life-supporting system, the ecosphere, and that we cannot survive outside of it. The sustainable use of natural resources, development that will no longer be harmful to the environment is the only possible solution. In our quest for reaching a sustainable way of life, biodiversity management and conservation arose as the major tools for reaching this goal.

Biodiversity made the headlines throughout most of the last decade, developing into a matter of high concern in most of the world. From a subject with little impact, of interest only to environmentalists and to parts of the scientific community, it rose to a high publicity issue. So what does biodiversity mean? Most people, especially biologists, are inclined to agree that it is, in one sense, everything. But since 'everything' is a bit too abstract, difficult to measure and to quantify, let's try to see how it can be defined and described in a measurable way.

The word biodiversity is a contraction of biological diversity. It was first used during the National Forum on BioDiversity held in Washington in 1986. The proceedings of the forum were published two years later under the title BioDiversity, and were later cited, most often inaccurately, as Biodiversity (Wilson, 1997). By 1992, at the United Nations Conference on Environment and Development in Rio de Janeiro, biodiversity became a major issue of concern worldwide. The Convention on Biological Diversity (CBD) was signed by 168 countries. Presently there are over 180 Parties through ratification after signature or accession (i.e. ratification without signature). There are three main objectives of the CBD: conservation of biodiversity, sustainable use of biodiversity, and the fair and equitable sharing of benefits arising from its utilization. Thus the key to maintaining biological diversity depends upon using it in a sustainable manner. More than a decade has now passed since the signing of the CBD and its entry into force (December 1993), and biodiversity is still a 'hot topic', drawing the attention not only of ecologists and biologists, but also economists, lawyers and politicians. This huge, unexpected 'success' of the term biodiversity is a result of our failure to manage and preserve our natural resources, most often focused only on species diversity. Biodiversity was the political response, bringing a more comprehensive approach in dealing with natural resources management and conservation issues. Perhaps the most important contribution made by 'biodiversity', is that it provides a basis for influencing the political process, and encourages those involved in conservation to look more seriously at the major aspects of concern (McNeely, 1998). In policy discussions, biodiversity covers a huge and heterogeneous array of topics, scales and questions.

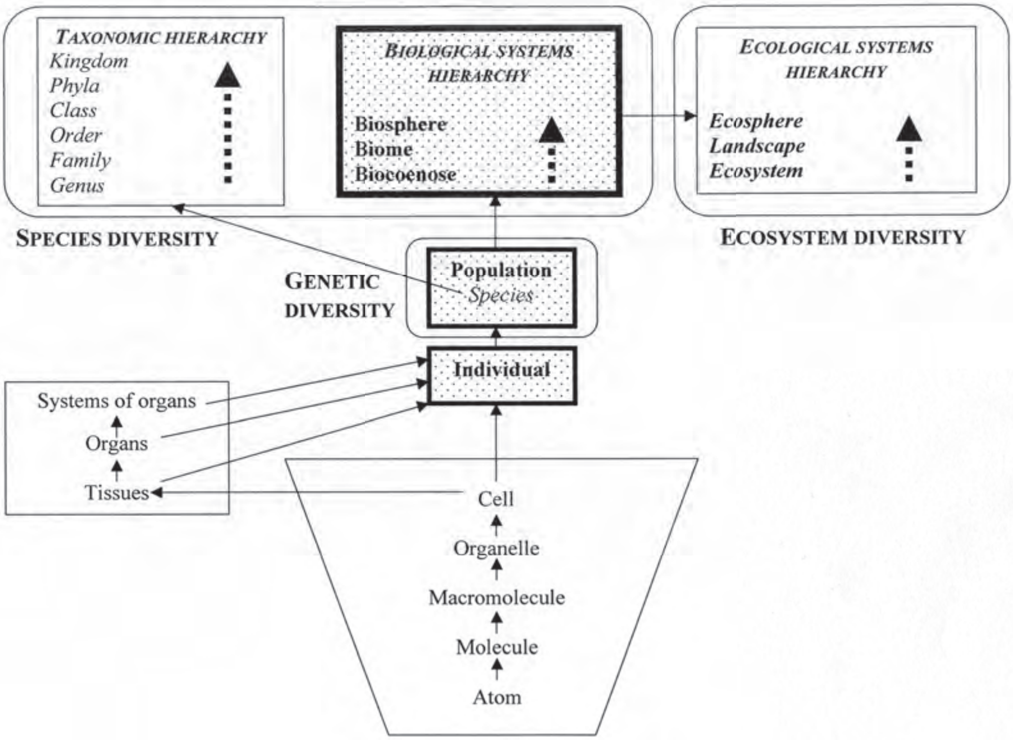


Figure 1.1 The hierarchical structure of the different components of biodiversity. The biological systems hierarchy is composed of at least five levels, ranging from individuals to the biosphere. Species diversity includes both the taxonomic hierarchy and the biological systems hierarchy (adapted from Botnariuc, 1992).

1.2 Components of biodiversity

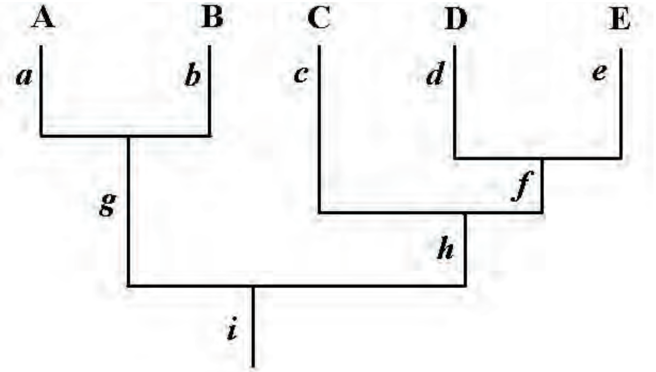
Diversity is a concept that refers to the range of variation or differences among some set of entities, being a measure of its heterogeneity. Biological diversity is the result of evolutionary processes during geological periods that generated the entire variety of biological and ecological systems, allowing the existence of life in a multitude of forms. Since biodiversity includes entities with varying degrees of complexity and different time-space scales it has a hierarchical structure. It includes the variety of components of the ecosphere, of the entire hierarchy of the biological and ecological systems (Figure 1.1). The hierarchy of biological systems covers several levels, starting with the individual and all the inclusive categories, representing increasingly complex forms of grouping individuals. Thus, individuals belonging to a species exist within a population. Populations within a habitat form a biocoenose. All the individuals inhabiting Earth are part of the biosphere.

The most often cited and used definition of biodiversity is that given in the Convention on Biological Diversity (Article 2): ‘Biological diversity’ means the variability among living organisms from all sources, including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. Apart from the legal definition, there is a wide variety of definitions of biodiversity, as reviewed by DeLong (1996). Some of the current definitions of biodiversity are presented in Table 1.1

Three main components are thus defined: genetic diversity (within species), species diversity, and ecosystem diversity. A fourth component is sometimes added, the ethno-cultural or human diversity. Several dozen definitions are in use (Table 1.1). The

Box 1.1 Phyletic diversity measurement

An interesting method of measuring the phyletic diversity of a subset of taxa was proposed by Faith (1995), as the sum of the lengths of the branches found along the path down the tree connecting all taxa in the subset, which assesses the amount of evolution accounted for. Thus, the phyletic diversity of all five taxa *A-E* equals the length of branches *(A-E)= a+b+c+d+e+f+g+h+i*, while for *A, B* and *C (A-C)= a+b+c+g+h+i.*



topic is further complicated since there is a variety of other terms referring to biological diversity that appear in the scientific literature, most of them as synonyms or measures of the three major components. For example, genetic diversity is sometimes measured or quantified as biochemical diversity. Species diversity is often estimated at higher taxonomic levels as taxic diversity, defined as a measure of the number of species, their taxonomic position and the different contributions that species makes. It can also be measured as the diversity of species within trophic levels (referred as trophic diversity), taxonomic groups, or even according to the size or growth form. Another frequently used measure of species diversity is taxonomic or phyletic diversity, which is a measure of the diversity of higher taxa within a group of species. Another measure of species diversity, focused not on sheer number (structure) but on the functions performed is functional diversity, which is defined in two different ways, either as the diversity of the ecological functions performed by different species, or as the diversity of species performing a given ecological function. Last, ecosystem diversity is sometimes referred to as system diversity, ecological diversity or habitat diversity (van der Maarel, 1997).

A biodiversity approach not only links species conservation with habitat and genetic conservation, but also addresses the political, social and economic factors involved. Due to its wide coverage, biodiversity cannot be directly studied as a whole, only at different levels of complexity (genes, species, ecosystems). Species are the most useful component in the study of biodiversity, since they represent its best reflection, are discrete entities, and there is at least a relative consensus regarding their definition and identification. Also the number of species can be (at least in theory) estimated at different spatial scales. Species are also good indicators of environmental stress, some of them provide key roles in the provision of ecological services and last but not least, individual species are the units of interest to people. There are also several drawbacks when focusing on species diversity since there is still no universal definition of species and the criteria used for describing species varies between higher taxa. Nevertheless, species diversity remains the major component of biodiversity on which most scientific, public and political issues focus. In this book, I will focus on species diversity and try to cover the most important aspects related to it.

Table 1.1 The diversity of definitions of biodiversity.

Biological diversity refers to the variety and variability among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequency. For biological diversity these items are organized at many levels, ranging from complete ecosystems to the chemical structures that are the molecular basis of heredity. Thus, the term encompasses different ecosystems, species, genes, and their relative abundance. **(OTA, 1987)**
Biodiversity is the variety of the world's organisms, including their genetic diversity and the assemblages they form. It is the blanket term for the natural biological wealth that undergirds human life and well-being. The breadths of the concept reflect the interrelatedness of genes, species and ecosystems. **(Reid and Miller, 1989)**
Biological diversity encompasses all species of plants, animals and microorganisms

and the ecosystems and ecological processes of which they are part. It is an umbrella term for the degree of nature’s variety, including both the number and frequency of ecosystems, species or genes in a given assemblage. **(McNeely et al., 1990)**

The genetic, taxonomic and ecosystem variety in living organisms of a given area, environment, ecosystem or the whole planet. **(McAllister, 1991)**

Biological diversity refers to the full range of variety and variability within and among living organisms, their associations and habitat-oriented ecological complexes. The term encompasses ecosystem, species and landscape, as well as intraspecific (genetic) levels of diversity. **(Fiedler and Jain, 1992)**

The structural and functional variety of life forms at genetic, population, species, community, and ecosystem levels. **(Sandlund et al., 1992)**

The variety of living organisms considered at all levels, from genetics through species, to higher taxonomic levels, and including the variety of habitats and ecosystems. **(Meffe and Carroll, 1994)**

Biodiversity is a state or attribute of a site or area and specifically refers to the variety within and among living organisms, assemblages of living organisms, biotic communities, and biotic processes, whether naturally occurring or modified by humans. Biodiversity can be measured in terms of genetic diversity and the identity and number of different types of species, assemblages of species, biotic communities and biotic processes and the amount (e.g., abundance, biomass, cover, rate) and structure of each. It can be observed and measured at any spatial scale ranging from microsites and habitat patches to the entire biosphere. **(DeLong, 1996)**

Biodiversity refers to the variety and variability among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequencies. For biological diversity, these items are organized at many levels, ranging from complete ecosystems to the biochemical structures that are the molecular basis of heredity. Thus, the term encompasses different ecosystems, species, and genes. **(EPA, 1997)**

The variety of organisms considered at all levels, from genetic variants belonging to the same species through arrays of species to arrays of genera, families, and still higher taxonomic levels; includes the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live. **(Wilson, 2001)**

Biodiversity refers to species, genetic, and ecosystem diversity in an area, sometimes including associated abiotic components such as landscape features, drainage systems, and climate. **(Swingland, 2001)**

Biodiversity is synonymous with species richness and relative species abundance in space and time. Species richness is simply the total number of species in a defined space at a given time, and relative species abundance refers to their commonness or rarity. **(Hubbell, 2001)**

1.3 What is a species?

Species are the basic unit of classification, consisting of a population or series of populations of closely related and similar individuals that freely interbreed with one another in natural conditions but not with members of other species. Species also have a historical continuity; they have existed in the past and unless they become extinct, will continue to exist in the future. They can be viewed as a channel transmitting genetic information in time through the component individuals.

Species are real, well-defined biological systems but nevertheless they are paradoxical entities. They are torn apart between the need to preserve their identity and travel through time without alteration (conservative), and the permanent changes due to mutations and recombinations (evolution) which cancel their initial identity (Botnariuc, 1992). There are several mechanisms and processes that operate at different levels of complexity and allow for their dual nature. At the genetic level, the redundancy of genetic information (i.e. double strand of DNA, double number of chromosomes in most species, complete genetic information within each cell of metazoans), the various DNA reparatory systems, and the semi-conservative mechanisms of multiplication/replication converge to the unaltered transfer in time of the genetic information. The opposing processes are mutations and recombinations, induced by a variety of factors that affect all levels of complexity of genetic information (codon, gene, chromosome, and genome). At the population level, panmixia (i.e. the random breeding among individuals within a population) is mitigated by a wide variety of mostly behavioral reproductive barriers that limit its importance. Dispersal, as a process that maintains cohesion among the populations belonging to a species, is often limited. Thus, species appear to be contradicting, unstable systems navigating between metastable phases.

1.4 Time-space scales in the study of biodiversity

Species are historical units, the result of continuous selective and adaptive processes. The footprint of this historical evolution is stored in the genotype. Species are not only following certain patterns of distribution in time but also in space, occupying ranges that vary in size between tens of square meters to millions of square kilometres. Present day biodiversity is the result of almost four billion years of dynamic evolution, during which the Earth suffered major changes, with entire continents rising and disappearing and billions of species that appeared and then became extinct in time. Natural changes are still taking place, but human influences are becoming dominant in major parts of the world. It is difficult to study and understand the complex patterns and mechanisms behind these dynamic processes, but certain general rules must be followed. Perhaps the first and most important is a correct scaling of the domain of interest, in both time and space.

Biodiversity has a many-fold importance to us, from local to global scales. Different processes operate at different time-space scales. It is therefore extremely important when attempting to study and understand the dynamic changes within the different components of biodiversity, to confine to a certain time-space domain.

The rising of the concept of scale in ecology has received increasing attention lately. Schneider (2001) reviews how the concept of scale became a central concern in ecology. The problem of scale arose because the major, pressing problems in ecology take place at scales of tens and hundreds of years, on areas that are millions of square kilometers large. Patterns measured at small spatial and temporal scales are often not valid at larger scales, nor do processes dominant at small scales necessarily prevail at larger scales. We are trying to address problems at larger scales by studying them locally, and frequently we are getting wrong or biased answers when up-scaling. To cope with the present biodiversity crisis we have to understand the time-space scale and the different patterns and processes operating within each domain (Table 1.2). With a correct understanding of scaling we can start asking pertinent questions and limit the validity of the answers obtained within their range of applicability (Figure 1.2).

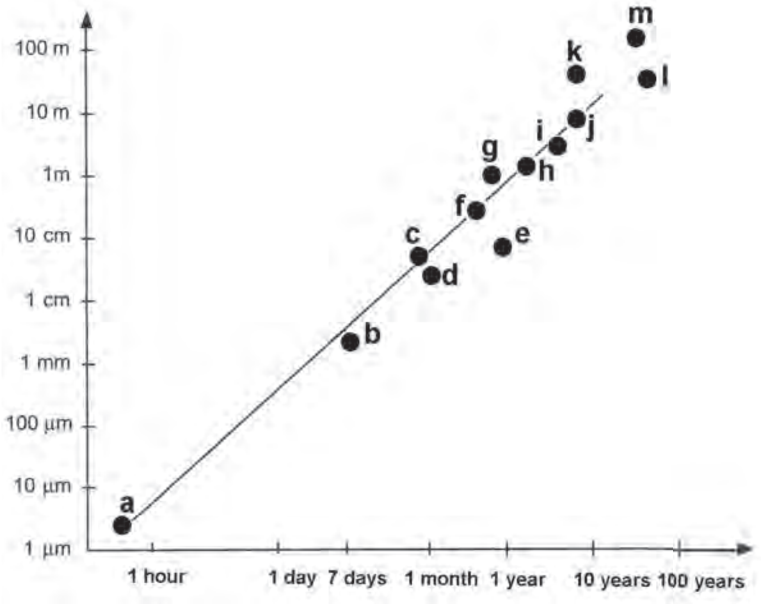


Figure 1.2 The size and generation time for different species along a logarithmic scale: (a) the protozoan; (b) aquatic water flee; (c) bee; (d) fly; (e) snail; (f) mouse; (g) rat; (h) fox; (I) deer; (j) rhinoceros; (k) whale; (l) birch tree; (m) pine tree (after Jørgensen and Svirezhev, 2004).

Table 1.2 The major time-space domains within biodiversity studies. Note that there is a certain degree of overlapping among the different domains.

Hierarchical units (biological/ ecological)	Scale domain	Space scale range (m^2)	Time scale range (years)	Disturbance process	Biotic processes	Discipline
Population/ habitat	Local	10^1 - 10^7	10^{-2} - 10^3	Epidemics	Population demographics	Population biology
Community/ ecosystem	Local	10^5 - 10^7	10^1 - 10^3	Periodic abiotic disturbances (e.g. fire regime, floods)	Ecological succession/ genetic variation	Ecology
Biota/Landscape	Regional	10^7 - 10^{10}	10^3 - 10^5	Extreme abiotic disturbances	Speciation and extinction	Landscape ecology
Macrobiota/ Biogeographical province	Macro-regional	10^{10} - 10^{14}	10^4 - 10^8	Climate changes	Evolution of biotas	Evolutionary biology / Paleontology
Biosphere/ Ecosphere	Global	10^{15}	10^5 - 10^9	Plate tectonics	Macroevolution	Life sciences

1.5 Genesis of biodiversity

Before discussing the dynamic chances in biodiversity at different time and spatial scales, a brief outline of how life developed on Earth is needed. Present-day biodiversity is the result of almost four billion years of evolution marked by innovative solutions and rapid forward leaps followed by long periods of stagnation. It all started about 4.5 billion years ago with the formation of planet Earth, a part separated from the sun, boiling at huge temperatures. In time it started to cool, allowing the formation of the atmosphere, then the lithosphere (the solid surface crust) and once the temperature dropped below 100^0C, the hydrosphere. At that time, everything was different from present, the oceans were very acidic and the atmosphere consisted mainly of carbon dioxide. The first living organisms appeared in the ocean about 3.5-4.0 billion years ago. They were bacteria like, lacking organelles and nucleus (prokaryotes), feeding on the organic compounds dissolved in water. Soon, i.e. more than 3 billion years ago, there was not enough food for all of them. Then, some turned towards a better source of energy, plentiful and unending, the solar radiation and started transforming and storing it as chemical energy through photosynthesis. Photosynthesis allowed the organisms to thrive on this huge source of energy, but also had a side effect that in time completely restructured the planet. During photosynthesis, water molecules are decomposed to use the hydrogen and the dangerous, extremely reactive compound previously bound to it, oxygen, is released as a gas. Introducing oxygen into the Earth's atmosphere was of major importance. It provided a fuel that would allow the evolution of more complex organisms with higher energy demands, but also represented a new source of toxins (Abele, 2002). Oxygen has the ability to form incompletely reduced reactive species which are highly potent, oxidants. They combine with a variety of substances and disrupt vital processes within an organism not provided with defense mechanisms. In time, oxygen accumulated in both water and air, and about two billion years ago, at less than 0.3% of its present concentration (Botnariuc, 1999), it was toxic enough and could not be ignored anymore. Instead of building further defenses against oxygen's toxicity, most living organisms started using its reactivity to further break down organic compounds and use more of the chemical energy stored, a process called respiration. A similar approach was used towards another highly toxic compound widespread in the environment, calcium, which was bound and inactivated and then stored within the body in special formations. Organisms started to make better and better use of calcium by constructing elaborate exoskeletons and later on endoskeletons, which eventually provided for most of the fossil record.

The more efficient oxygen-burning cells grew faster and in time, started to include other cells within their own membrane, cells that became specialized either in photosynthesis (plastids), or respiration (mitochondria), a process named endosymbiosis. A primary function of mitochondria may have been to compartmentalize respiration, thus protecting the cell from the dangerous side-effects of oxygen metabolism (Abele, 2002). This is how the first eukaryotic organisms were formed about 1.8 billion years ago (Margulis, 1992). About 1.1 billion years ago, the simple asexual reproductive strategies were replaced with a more complicated process, derived from the DNA repairing mechanisms, named sexuality (Margulis and Sagan, 1986). After a couple of hundred million years, the first metazoans (i.e. multicellular) algae were recorded from the fossil record, followed around 600 million years ago, by the first invertebrate metazoans (Schopf, 1994). Then a burst in speciation occurred, with new and innovative plans of organization arising, and with a huge diversity of phyla emerging. The most important and impressive burst of speciation occurred at the beginning of the Cambrian. This process can be divided in three different stages (Philippe and Adonette, 1996). The initial Precambrian fauna, most probably diploblastic (i.e. having body parts derived from two layers during embryologic development) appeared during 570-555 million years ago, and by the early Cambrian (about 540 million years ago), most organisms were already triploblasts (i.e. having body parts derived from three layers during embryologic development), followed by the explosive diversification of this fauna in the middle Cambrian (about 520 million years ago). Thus, it appears that the major diversification of metazoans into more than the 35 extant phyla, since several lineages were later eliminated, may have occurred in less than 20 million years. The first primitive fish, animals with internal skeletons (i.e. vertebrates), appeared about 500 million years ago. Then a huge increase in species diversity occurred by growing command of the Earth's environment. Plants were already producing large amounts of oxygen, so its concentration in the atmosphere reached a concentration similar to the present-day one. When at high altitude in the atmosphere, the oxygen molecule (O_2), consisting of two oxygen atoms, can be broken apart by the high-energy content of ultraviolet (UV) radiation. The resulting oxygen radicals are extremely reactive and can combine with an oxygen molecule generating a compound called ozone (O_3). Ozone can absorb UV radiation and in time, the large quantities of ozone accumulated in the higher strata of the atmosphere, tens of km above the surface, created a shield against the harmful effects of this radiation. Until then, life forms existed only in water, which could shield them from UV radiation. Land was a barren, scorched, desert-like structure, deprived of any life forms. Thus organisms managed to alter the world to better suit their needs.

About 440 million years ago, the first plants, followed by invertebrates and vertebrates, started colonizing the land that was safe then from UV radiation. It was not an easy task since water is 775 times denser than air and aquatic organisms have adapted by having a specific gravity just slightly higher. They needed no supporting tissues or supporting organs, which are used, when present, only to assist in movement. On the other hand, movement in water requires more energy than in air (Dobson and Frid, 1998). Furthermore, life on land was controlled from the very beginning by a vital, limiting resource, which was water. Colonizing organisms, deserting the aquatic environment, had to adapt and limit water losses by insulating their external parts, by developing storing formations and by reducing water needs and consumption. The harsh terrestrial environment put a tremendous pressure on the organisms that attempted to colonize and adapt to it. There was nevertheless a powerful motivation to do it, since the slow fusion of continents into a single land mass (Pangaea) reduced severely the length of coastline and coastal habitat availability. Not all marine phyla attempted or succeeded in doing so. It is also estimated that oxygen levels in the Devonian and Carboniferous periods were much higher than now, reaching almost 35% compared to the present level of 20%. This allowed animals to grow much larger and quicker than now (Officer and Page, 1993).

Although now there are more terrestrial than aquatic species, the complexity of life forms is lower on land. The most successful group that developed on land in an enormous variety of similar forms is the insect. Plants had to develop huge skeletons consisting of cellulose and lignin to fight gravity, and had to adapt to the limited water supply by developing a pumping system in their roots that could send water, sometimes tens of meters high, against the gravity pull. The large amount of organic matter stored in woody structures was mostly unavailable to usual grazers and herbivores, and accumulated in enormous quantities, partly contributing to the formation of soils, while others in time transformed into coal. In this way, huge amounts of carbon dioxide were pumped from the atmosphere and caused a decrease of the greenhouse effect, inducing the first biotic-driven climatic changes. At this stage, all the surface of the planet was already covered by life forms, generating the newest layer called the biosphere. Then, about 200 million years ago, plate tectonics accounted for the steep rise in diversity. This was due to fragmentation of the Earth caused by the break-up of Pangaea, the only supercontinent existing, and the rise of the sea level (Briggs, 2005). This formed a variety of terrestrial and aquatic biogeographical barriers that effectively isolated previously connected populations and thus increased the rate of speciation. Last but not least, during the last several thousand years humans have drastically modified the environment, severely depleting species diversity.

The present-day biodiversity is the result of a long process of evolution that we have just started to understand. In the next chapter, I will try to summarize in the next chapters some of the major processes responsible for the dynamics of species diversity.