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Core Concepts in Studying Ecology and Evolution

The study of microbiology, ecology, and evolution is extremely broad. Entire textbooks and sets of textbooks have been written on each subject. There are numerous scientific journals that continue to expand our knowledge of each of these subjects. Numerous annual, semi-annual, and special scientific meetings are held in which cutting-edge science is presented and discussed. Specialists spend their careers examining and describing subsets of only one of these disciplines. However, an understanding of basic underlying principles of biology requires that efforts be made to see linkages among disciplines and to meld the theories and insights of one discipline with those of another. It is beyond the scope of this text to present in detail many of the aspects of each of these disciplines. In this introductory chapter we will briefly cover some of the major topics belonging to each discipline as an introduction to the material that will follow.

The Beginnings of Microbiology

Although van Leeuwenhoek described microbes during the 16th century with his ingenious microscopes, little was done to understand these very small organisms for many, many years. Van Leeuwenhoek's observations using his microscopes surpassed all other observations for over 400 years. Although not formally trained as a scientist, van Leeuwenhoek had a natural propensity to ask questions about various substances and samples and then examine many different types of samples. He studied river, pond, well, and seawater. He described the microbiota of spittle and teeth tartar, and he was the first to see sperm cells.

Unfortunately he left no descriptions of his apparatus with which he was able to observe both protozoa and bacteria. His descriptions of various organisms were so exact that we can almost assign taxonomic affiliations based just on the descriptions. His observations are so good that he must have had novel means of illuminating his subjects and he probably discovered dark field microscopy, a practice still used today. Although van Leeuwenhoek made observations of many different types of samples for over fifty years and wrote over 150 letters to the Royal Society of London little attention was paid to these marvelous little creatures for a considerable length of time.

It was not until several centuries later that scientists began to ask questions about these organisms. Among the first questions was whether these microorganisms could arise through spontaneous generation. Although Redi had proved that maggots in meat arose from flies, there was no definitive proof that microbes could not come into existence spontaneously. Redi had excluded the adult flies using gauze with a weave that prevented the adult flies from *ovipositing* their eggs on the meat. However, although they did not know how microorganisms came into being, no gauze would have been fine enough to prevent microbes from colonizing the meat. It was not until Pasteur that the source of many microbes in contaminated substances was understood. Pasteur's experiments were a masterpiece of logic and experimentation. However, his results did not completely destroy the idea of spontaneous generation. It was not until Tyndall demonstrated that sterilization of various materials required different means that spontaneous generation was laid to rest. Tyndall was able to completely sterilize the starting broths or infusions from a variety of substances and by so doing eliminated all subsequent growth.

Formal microbiology has its origin in the discoveries of the 19th century that began to reveal the existence and importance of many organisms too small to see. Today through the creative insights and persistence of numerous scientists the role these tiny organisms play in disease, various nutrient cycles, the food industry, and their nearly global distributions have been worked out. Microorganisms were found to be everywhere the scientists were creative enough to sample. However, outside of medicine, few other studies were done to understand what role these creatures played and more exactly who the organisms were that were involved. Microorganisms were obviously too small to be of much importance and they were extremely difficult to study.

Fortunately, people do not like to be sick. It is this disposition that gave impetus to the study of disease causing organisms. In the process, many capable scientists have contributed to our understanding of microorganisms. They have formulated and developed methods and resources for the systematic study of microorganisms and, in so doing, have provided a wealth of information on the genetics, physiology, and to some degree the behavior of disease causing organisms. They have discovered ways to isolate, characterize, and recognize various microbes. The isolation of disease causing organisms has been the mainstay of microbial taxonomy. Although much effort has been made in understanding disease-causing organisms in a host, very little effort has been made to study the ecology of disease causing organisms outside of the hosts. This is an area waiting for clever scientists to study.

Understanding both ecological and evolutionary concepts is critical in attempting the study of organisms in nature. Unfortunately, microorganisms have not been the subjects of ecological or evolutionary studies to any great degree. Perhaps our inability to really cure microbially induced diseases is a function of our lack of understanding of the basic *natural history* of these organisms. In one sense the realization that the strains of viruses that cause influenza differ among themselves and may differ even within a strain over time is a first cut at considering the evolution and ecology of these organisms.

This chapter presents a brief natural history of two major classes of microbes: viruses and bacteria. These groups are too broad and diverse to present much information in detail but this information will form a basis for much of what follows. Although there is a rich literature on microbial eukaryotes, little attention will be paid to these organisms except in their interactions with viruses and bacteria. Exceptions will include some discussion of some fungi.

Viruses

Viruses are curious things. They have been the subjects of much debate as to whether or not they are even alive. The reader is asked to review any beginning biology textbook to get the basic arguments for or against viruses being alive. Regardless of what the textbooks say, viruses have interesting life histories, and some of the main properties of living things (i.e., genetic material and genetic change) are integral to the biology of viruses. Interactions between the host and a virus are essential in understanding the ecology and evolution of viruses. This is because viruses are obligate intracellular parasites. Outside of a host, viruses do not fit the classic definition of an organism because there is no metabolism, they do not reproduce themselves, they do not take energy from the environment, and they do not respond to stimuli. However, within a host, viruses demonstrate many of these properties.

Viruses are small. They range in size from 0.02 to 0.2 μm and are composed of a protective protein covering that surrounds a very small amount of nucleic acid (DNA or RNA) in quantities ranging from a few to several tens of kilobases. This genetic information is enough to code for only a handful of proteins. Even though they have such little genetic information, they are highly adaptable and maintain high levels of genetic diversity. Despite their extremely small size, there is a diversity of shapes found among the viruses (Figure 1.1).

The basic steps in viral replication are similar for all viruses whether they infect plant, animal, or bacterial cells. Viruses can only infect cells in which there are chemical structures on the surface of the virus and the host cell, which permit attachment and penetration. How many types of cells (or the host range) a particular virus can infect is determined by these receptor-dependent interactions.

The first step in a viral infection is for the viral nucleic acid to get into a cell through penetration of the host cell surface. For some viruses penetration is facilitated by release of an enzyme located in the phage tail that degrades a small part of the cell wall. The nucleic acid is then literally forcibly injected into the cell. Then replication of viral nucleic acids and the synthesis of viral constituents take place using the cell's anabolic machinery.

There are three different outcomes that can come from an infection: the infecting viruses multiply into many progeny which kill and lyse the host cell releasing the newly made viruses into the environment; the viruses multiply into many progeny within the host but the host cell does not lyse and the cell survives; and a stable condition is established with little or no viral multiplication and where the virus is integrated into the cell's genome or it remains as a separate entity within the cytoplasm of the cell.

Virus or virus-like particles can reach very high densities in the environment. These densities are probable sufficient to expose many bacteria and eukaryotes to viral infection. As will be seen in later discussion viruses may actually regulate microbial populations in nature to some extent.

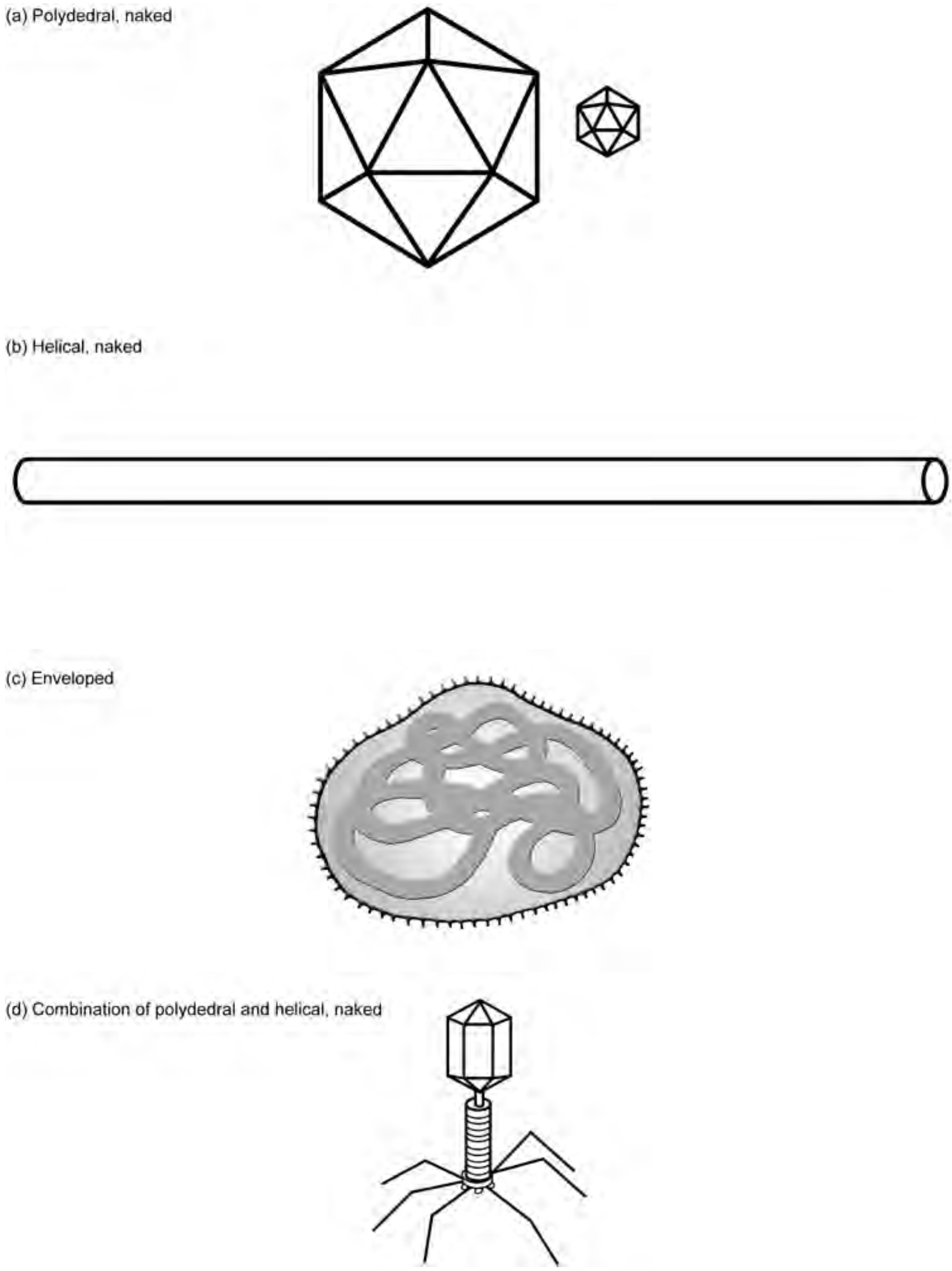

Figure 1.1 Different shapes of viruses or virus-like particles: polyhedral (**a**); helical (**b**); enveloped (**c**); and combination (**d**). (From Nester EW, Roberts CE, McCarthy BJ, Pearsall NN. *Microbiology: Molecules, Microbes, and Man.* New York, Holt, Rinehart & Winston, 1973.)

Bacteria

Bacteria are among the most diverse if not the most diverse groups of organisms found on the planet. Attempts to classify these organisms using culturing techniques have resulted in more than 3,000 named bacteria. Because there are more than 600,000 species of beetles, this statement of being the most diverse group seems a little rash. This number of species is woefully small, and research using culture-independent techniques have demonstrated considerable diversity (discussed later). The purpose of this text is not to describe the various groups of microorganisms in any definitive manner. Because the main text does not discuss specific groups of bacteria except as they relate to specific topics, the major groups of bacteria are briefly mentioned here. Table 1.1 summarizes some of the differences found among the major groups of bacteria. Much more complete descriptions are given in many microbiology textbooks and these should be referred to for additional information. Our purpose here is to review these groups as an indicator of the wide diversity of bacteria found on the earth. Although the source for these comparisons and description comes from a work written in the 1970s, most of these groups were observed in the 1600s, and little new morphological information can be found. Rather considerable differences have been found in subcellular constituents in recent years.

Photosynthetic Bacteria

All major morphological types of bacteria are represented among the photosynthetic bacteria: rods, cocci, and helical forms suggesting that photosynthesis among the bacteria is derived from diverse evolutionary origins. Some of the oldest fossils resemble blue-green or cyanobacteria. The details of bacterial photosynthesis are presented in the following section. Photosynthetic bacteria are found in wet soil, and both freshwater and marine habitats that lack oxygen but where light can penetrate.

Gliding Bacteria

These bacteria, as their grouping suggests, have the ability to glide or slide over solid surfaces. They lack flagella. There are several interesting taxa associated with this group that are found in a wide variety of habitats. Some of these habitats include the inside of the mouth, polluted rivers, sulfur springs, black mud, manure, decaying organic matter, and soils. As one might expect when a grouping is done on a phenotypic trait like gliding many different and distantly related organisms will be grouped together. This is true of the gliding bacteria.

Some of the species can form long filaments composed of chains of cells that are encased in a common wall. These filaments are not mobile; however, short segments can be. Other multicellular forms can be found including species found in the mouth and on decaying organic matter.

Sheathed Bacteria

The sheathed bacteria are another group of multicellular organisms that live in filaments. These filaments differ from those discussed in the previous section in that the filaments are enclosed in a sheath of lipoprotein-polysaccharide that is chemically different from bacterial cell walls. These organisms can increase to very high densities, especially below sewage outfalls.

Table 1.1 The Major Groupings of Bacteria and Their General Characteristics

Bacterial Group	Mode of Motility	Morphology	Nutrition	Staining	Other Features
Photosynthetic					
Purple, sulfur	Flagella, if motile	Rods, cocci, and helices	Phototrophic; autotrophic	Gram-negative	Sulfur granules deposited intracellularly
Green, sulfur	Flagella, if motile	Rods	Photosynthetic, autotrophic	Gram-negative	Sulfur granules deposited extracellularly
Purple, nonsulfur	Flagella, if motile	Rods, helices	Phototrophic, heterotrophic	Gram-negative	No sulfur granules
Gliders					
Filamentous sulfur	Glide on solid substratum	Multicelled filaments	Oxidize reduced sulfur compounds	Gram-negative	Sulfur granules deposited intracellularly
Nonfruiting mycobacteria	Glide on solid substratum	Long rods	Heterotrophic	Gram-negative	
Fruiting myxobacteria	Glide on solid substratum	Short rods that form microcysts	Heterotrophic	Gram-negative	Forms elaborate fruiting structures
Sheathed	Flagella	Multicelled filament enclosed in sheath	Heterotrophic	Gram-negative	Sheath
Prosthecate and budding	Flagella, if motile	Unicellular rods, vibrios, cocci, some have appendages and some divide by budding	Heterotrophic	Gram-negative	
Spirochetes	Axial filaments	Helical; flexible wall	Heterotrophic	Too thin to stain well	Cell is flexible and bends easily
Spiral or curved	Flagella, if motile	Bent rods or helical; rigid wall rods	Heterotrophic	Gram-negative	Cell is rigid and does not bend
Strictly aerobic, Gram-negative rods	Polar flagella if motile		Heterotrophic, nonfermentative	Gram-negative	
Facultatively anaerobic, Gram-negative rods	Polar or peritrichous flagella if motile	Rods, some very short	Heterotrophic	Gram-negative	Many pathogens, enterobacteria
Strictly anaerobic, Gram-negative rods	Polar flagella if motile	Curved and straight rods, some spindle shaped	Heterotrophic	Gram-negative	
Nonphotosynthetic autotrophs	Flagella	Rods, spheres, helices	Use CO_2 as major carbon source	Gram-negative	Reduced inorganic compounds supply energy
Gram-negative cocci	Nonmotile	Spherical found in pairs	Heterotrophic. Parasitic and pathogens	Gram-negative	Includes causative agents of gonorrhea and bacterial meningitis
Gram-positive cocci	Nonmotile	Spherical, chains, packets or clusters common	Heterotrophic	Gram-positive	Includes important pathogens
Endospore formers	Peritrichous flagella if motile	Rods	Aerobic, facultative or anaerobic heterotrophs	Gram-positive	Spore is very resistant
Non–spore-forming, Gram-positive rods	Peritrichous flagella if motile	Rods	Heterotrophic	Gram-positive	Diverse group
Branching	Flagella, if motile	Branching rods and nonseptated filaments; some produce spores on aerial hyphae	Heterotrophic	Some acid fast	Includes important pathogens
Mycoplasmas	Nonmotile	Irregular shape due to absence of cell wall	Heterotrophic; most require sterols	Gram-negative	Only prokaryotes with sterol-containing cytoplasmic membranes
Obligate intracellular	Nonmotile	Small, short rods	Heterotrophic. Must grow intracellularly	Gram-negative	Some have leaky cytoplasmic membrane

Adapted from Nester EW, Roberts CE, McCarthy BJ, Pearsall NN. *Microbiology: Molecules, Microbes, and Man.* New York, Holt, Rinehart & Winston, 1973.

Budding and Prosthecate Bacteria

These organisms have appendages that project out from the bacterial cells. The prosthecae are the stalks by which some of these bacteria attach to surfaces by adhesion by a holdfast located in the tip of the appendage. The prosthecae are actual extensions of the bacterial cell and contain cytoplasm. Budding bacteria may or may not attach to surfaces. Their unique characteristic is the ability to reproduce by budding.

Spirochetes

The spirochetes are also grouped based on morphology. The specific morphology is helical or wave shaped. These organisms have flexible cell walls and are capable of movement using axial filaments. These organisms are found in aquatic habitats and as parasites of warm-blooded animals. Van Leeuwenhoek probably observed some of these organisms as indicated by his drawings.

Spiral and Curved Bacteria

We might expect that a spiral shaped bacterium be grouped with the spirochetes but such is not the case. These organisms are much larger than the spirochetes and they have a rigid cell wall. Some of these organisms are predators of other bacteria and will be discussed in more detail in later chapters.

Strictly Aerobic Gram-Negative Rods

This is one of the large "cover-everything" type groups. These organisms are Gram-negative rods. In fact it contains one of the best-known groups: the pseudomonads. This group by itself is interesting because the name literally means false unit (Latin *pseudo* = false, *monad* = unit). These organisms are characterized as being motile by polar flagella. They live in just about every habitat that has ever been sampled. Some members of these strictly aerobic organisms can fix nitrogen while others are known parasites of humans and animals.

Facultative Anaerobic Gram-Negative Rods

This group is characterized by the ability to ferment carbohydrates. Many bacteria found in the guts of other organisms are within this group (e.g., *Escherichia coli*, many plant and animal pathogens). Some of these pathogens are responsible for plague.

Strictly Anaerobic Gram-Negative Rods

These organisms are important both as free-living forms and as pathogens and parasites of man. The upper respiratory, gastrointestinal and lower urogenital tracts usually have high numbers of these organisms. In nature members of this group perform part of the sulfur cycle.

Nonphotosynthetic Autotrophic Bacteria

Nonphotosynthetic autotrophic bacteria generate energy by oxidizing inorganic compounds rather than by using organic matter. As with all man-made groupings, some of these organisms can be classified with other groups. This includes members of this group that are also gliding bacteria. Some of these bacteria are involved in the sulfur cycle and actually produce sulfuric acid. Others can oxidize reduced iron and fix carbon dioxide, and still others of this group can reduce carbon dioxide to methane and are found in the digestive tracts of cattle or other animals or in the anaerobic mud of marshes and wetlands.

Gram-Negative Cocci

Gram-negative cocci can be commonly found associated with animals but rarely in the external environment. Members of this group cause gonorrhea and meningitis. They can be either aerobic or anaerobic.

Gram-Positive Cocci

The Gram-positive cocci are important in industry and food processing, as well as extremely difficult to control disease-causing bacteria. Some members of this group have developed multiple resistances to a wide variety of antibiotics.

Endospore-Forming Bacteria

Endospores are mostly formed by Gram-positive rod-shaped bacteria that are commonly found in soils. Some require anaerobic conditions while others can grow in air. The endospore is a structure that allows survival during adverse or harsh conditions (discussed later).

Non–Spore-Forming, Gram-Positive Rods

The non–spore-forming, gram-positive rods are very widespread and have representatives from a number of bacterial taxonomic groups. Some are found in the mucous membranes of humans. Others inhabit soils where they are capable of breaking down complex man-made compounds such as insecticides and herbicides.

Branching Bacteria

Some bacteria grow by extending mycelia into their growth medium. They produce many types of antibiotics and are important in the degradation of lipids and waxes in plants and animal tissues. Others are widespread in soils and give soil its distinctive odor. This group includes both Gram-negative and Gram-positive organisms and several novel and interesting modes of reproduction.

Obligate Intracellular Bacteria

This is a group that is receiving considerable attention recently. Some of these bacteria are capable of altering the behavior or the gender of the organisms they inhabit (discussed later). These organisms are transmitted during reproduction of the host and do not have a free-living form.

We have just barely touched on some of the wonderfully unique aspects of these amazing microorganisms. In so doing, it is important that we consider why and how this diversity in form and function arose and is maintained. Organisms live somewhere. In the process of living, they are affected by their environment, and in most cases, they are capable of modifying their environment to a greater or lesser degree. Evolutionary science is the study of how organisms change over time. Ecology is the study of organisms in their environments. We briefly review the sciences of ecology and evolution as preface to our in-depth study of microbial evolutionary ecology.

Ecology Becomes a Science

Ecology or the study of the factors that control the distribution and abundance of organisms began in the early 20th century. Ecology has its roots in *natural history*. Natural history is the knowledge of organisms in their environment. Where, when, and how to find various creatures were the questions that formed the basis of natural history. Ancient human tribes were well acquainted with the movements of various creatures, and where and how to find important plants. Plagues of insects and other organisms were frequently encountered and required explanation. However, the possible explanations were beyond the scope of experimentation and often included supernatural explanations.

As man became more interested in why certain plants or animals were found in specified locations and not elsewhere *biogeography* began to be studied. Biogeography was initially concerned with distributions of organisms over broad geographical scales—like continents or islands. Both botanists and zoologists were concerned about such patterns but they differed in their approach and interests. Students would be advised to study the history of ecological thought as it developed among botanists and zoologists. However, an exhaustive history of the science of biogeography is beyond the scope of this introductory material. Suffice it to say that there was major controversy between the two disciplines.

Early in the past century and accelerating during the 1950s and later, various theoretical concepts began to be developed by botanists and zoologists. Unfortunately, most of this thought was geared toward trying to understand the distribution and abundance of organisms that could be easily, or without too much trouble (e.g., insects), be observed without aid. Microbes, if they were considered at all were thought of as decomposers and lumped together as a single taxonomic and functional unit. Even this limited acknowledgment was flawed as scientists failed to grasp the magnitude of microbial processes or the level of microbial diversity. Exceptions were found in medicine in which scientists and health professionals sought to eliminate worldwide epidemics such as polio and smallpox. The recognition of modes of dispersal of pathogens and the observation that these same organisms were being encountered on a worldwide basis required significant improvement in isolation and identification techniques.

Ecologists have made significant strides in describing factors and processes that determine the distribution and abundance of the earth's biota, especially the macrobiota—plants and animals. In contrast to other scientists, who can perform most of their experiments in the laboratory under tightly controlled conditions, ecologists study perhaps the most variable of all subjects—nature. Nature is inherently messy, and variance is the rule. No two ecosystems are exactly alike. No two samples, even if taken very close to each other either in space or time, are exactly alike. The beauty of extremely controlled and replicated experiments is difficult if not impossible to obtain in ecological studies. Exceptions include greenhouse studies and *microcosm* or *mesocosm* studies in which the variability of nature is controlled through simplification. In these types of experiments, researchers are able to control some of the variability by reducing the complexity of the experiment. Single-species responses to various treatments are found in many greenhouse studies on plants. Mesocosm and microcosm studies often involve a small subset of species that may interact and under a much narrower set of environmental conditions than those found in nature.

Any field study has various levels of uncertainty associated with every variable measured. Most of these variables change both spatially and temporally. Nevertheless, ecologists have through various methods and approaches successfully completed numerous studies that detail processes and events that occur in nature. The beauty and intricacies of these processes and events is exceptional. The cleverness of the scientists is profound at times. These scientists have given incredible insight into the workings of nature for many organisms in many parts of the world.

It has been said that ecology is the painstaking description of the obvious. In other words, almost anyone can see patterns in nature but most are unable to explain why these patterns should exist. For example, the grasslands of the United States have few trees—why? The observation is open for everyone to see who passes through grassland. Ecologists attempt to answer such questions.

Ecology as a discipline spans scales from molecules to the biosphere and everything in between. Ecology may be concerned with chemical and organismal interactions or organism-to-organism interactions. Ecologists may seek to understand a single species or try to explain why certain groups of organisms are found together. Some ecologists measure the dynamics of important plant nutrients as a means of understanding the roles plants, animals, and the abiotic environment have on these substances. In reality, only ecologists who work with higher, easily seen organisms are explaining the obvious. Many ecologists study things that most people have never imagined or observed.

Over the past century, it has become clear that much of what determines distributions and abundances of even higher organisms is not readily visible. Such things as nutrient availability, temperature, pH, redox potential, moisture, and many other variables also affect where organisms are found. Variability within each of these abiotic variables has resulted in incredible levels of biological diversity both within taxa and among taxa. Biological variability includes such things as behaviors, mating systems, competitive ability, predation, population dynamics, community interactions, and many others.

Ecology is not just a descriptive science but involves carefully planned and executed experiments that have helped tease apart some of the relationships mentioned in the previous paragraphs. Ecology has a rich body of theory and an ever-expanding corps of researchers that have interests in all types of organisms and habitats in pristine, extreme, and heavily perturbed environments.

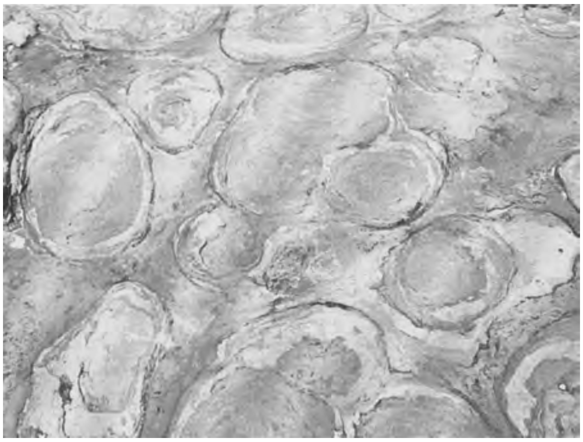

Figure 1.2 Fossilized cyanobacterial-like microorganisms. (From the National Audubon Society Collection/Photo Resesearchers and K. and B. Collins, Visuals Unlimited.)

Evolution

The oldest fossils discovered resemble bacteria that are found today. These fossils look remarkably like certain cyanobacteria (Figure 1.2). Other fossil microbes bear a strong resemblance, at least in outward morphology, to other bacteria that are present among us. These earliest known organisms are over 3 billion years old. Microbes have not changed in their physical outward appearance for a very long time.

Evolution in its simplest definition is change. However, that definition can be applied to many different systems, including living and nonliving systems. In biology, evolution is change that is transmitted through generations or, as stated by Futuyma, "descent with modification and often with diversification." Evolution is driven by a process called *natural selection* that is discussed later. Natural selection acts on the differences found among individuals that affect the rate of survival and reproduction.

Evolution by natural selection is based on four points that were made by different people but eventually summarized by Charles Darwin. These four points are

1. The offspring of an organism is more like the parents than any other organism. In other words, *like begets like*.
2. In every population of organisms, there are variations that have occurred by chance, and these variations are heritable or can be passed on through reproduction. These chance differences are the products of mutations that occur in the genes. However, Darwin did not know about DNA, RNA, and protein synthesis.
3. Most species produce more offspring than can actually survive and reproduce. Compared with the number produced, the number of organisms that actually reproduce may be very small.
4. Which organisms reproduce and produce viable offspring is in part determined by the action of their environment on chance variations produced by mutations. Over many generations, these favorable mutations will accumulate, and the population will be different from the original population and, on average, made up of more individuals with the favorable mutation.

Anyone who has been to a natural history museum can readily see that for some organisms, there is an incredible and often dramatic change in form and often function over the millions of years of the fossil record. Most species that have existed on this planet are now extinct and the extant species are a paltry subset of the diversity that has at times been found. However, where lineages are known or suspected, the visual representation of evolution is impressive and awe inspiring.

We began this section by observing that the microbial fossil record appears to show that for these organisms form has changed little over billions of years. Now it must be pointed out that fossilization of organisms is a chancy business at best. Even for large, hard-bodied creatures, the chance of being fossilized requires the organism to die in the right place; a place where geological processes can capture an image of the creature. For soft-bodied organisms that decompose rapidly, fossilization is a very chancy thing. For microbes, scientists must be able to recognize a microscopic fossilized body from the other components of the rocks. This is no small task (no pun intended). However, the fact that outwardly the known microbial fossils resemble the living organisms is interesting. For some microbial life, outward morphology has not changed for billions of years.

If we cannot observe physical differences among most fossilized microbes, why should we study the evolution of microbes? That is the rest of the story! Microbial evolution in the past and microbial evolution today have resulted in an incredible array of organisms, functions, and abilities to survive. Knowing something about how that diversity in species, functions, and abilities arose is important for understanding microbial life. Such knowledge can aid researchers in predicting various interactions that may aid in the clean-up of toxic wastes, in helping increase soil fertility, in industrial applications. Because microbes have been evolving longer than all other organisms put together perhaps we can learn more of the process of evolution by studying microorganisms.

Natural Selection

Not all individuals are able to reproduce at the same rates or levels in every generation and leave copies of their genes in the next generation. Nonrandomness in reproduction is natural selection. If there is a random effect, each individual, regardless of whether it was better adapted than another individual, may not reproduce simply by chance. Random effects could eliminate the best-adapted organisms simply by chance. However, if some organisms can leave more copies of themselves in the next generation than another organism then they will have somewhat of an advantage in the next generation.

Natural selection can act on all phases of an organism's life, including fertilization, development, growth, and sexual maturity. At every stage of life, various selective agents can act on the individual through disease, predation, and parasitism, as well as developmental or physiological problems. Differences in the ability to withstand or avoid these selective agents are a function of the genetic make-up of the organism. Mutations cause changes in alleles, and if favorable, they are retained; if not, the mutation and the individual are eventually eliminated.

Any individual or line of individuals that increase in number relative to others in the population will have more copies of their genes and will affect natural selection.

Fecundity is the number of offspring surviving into the next generation. Sometimes it is advantageous not to produce the most offspring. If producing more offspring means less maternal investment, fewer offspring may result in increased survival. For example, many species of birds spend considerable amounts of time finding food and then feeding their offspring. If these birds had too many chicks, they would not have the time or the energy to find the required food items, and all the chicks could perish. Having fewer offspring in this example means a higher likelihood that some of the offspring survive.

There seems to be a negative relationship between the numbers of offspring and the overall chances of survival. In general this relationship can be stated as high fecundity = low survival and low fecundity = high survival rates of offspring. For example, humans produce few offspring with fairly high levels of survival, but fruit flies produce many offspring, each with a low probability of survival.

In sexually reproducing organisms, not all of an organism's genes are passed on to the next generation. All of the genes are found somewhere in the gametes but not together. Sexually reproducing organisms leave only a haploid version of their genome in their offspring. Consider a heterozygote that has two different alleles, *T* and *t*. If every gamete has a 50 : 50 chance of getting one of the alleles, there is the same 50 : 50 chance that one of the alleles will not be passed on to the next generation. If a population is large, these losses by one individual are compensated by another such that the overall frequency of alleles remains fairly constant, though not an exact replica, between generations. In small populations there is an increased chance of what is called a sampling error or *genetic drift*. When the populations are small one of the alleles may be completely lost from the population by chance alone. In other words, natural selection does not bring about the change in gene frequency but rather random events do. The effects of genetic drift may be considerable especially if we consider that many populations of higher organisms are small and isolated from each other (isolation is discussed later).

Patterns of Selection

Because an organism can survive in a particular location, it is not an indication that natural selection has favored that particular genotype. The organism must be able to reproduce in the habitat. If the organism survives only as an individual and never reproduces, it is in reality poorly adapted. Natural selection does not measure the survival of individuals, but rather the ability of various organisms to leave the most offspring that can continue to reproduce. *Fitness* is a measure of the number of offspring produced by one individual genotype relative to that produced by another genotype.

There are basically three ways that selection can act within a population that result in a change in allele or gene frequencies as observed as changes in phenotypes. These three ways are *directional selection, stabilizing selection,* and *disruptive selection*. Each of these patterns is shown graphically in Figure 1.3. In general, directional selection favors one extreme phenotype; stabilizing selection occurs if an intermediate phenotype is favored, and disruptive selection occurs when two or more phenotypes are fitter than the intermediate phenotypes. The relationship between fitness and the phenotype is called the *selection regime*.

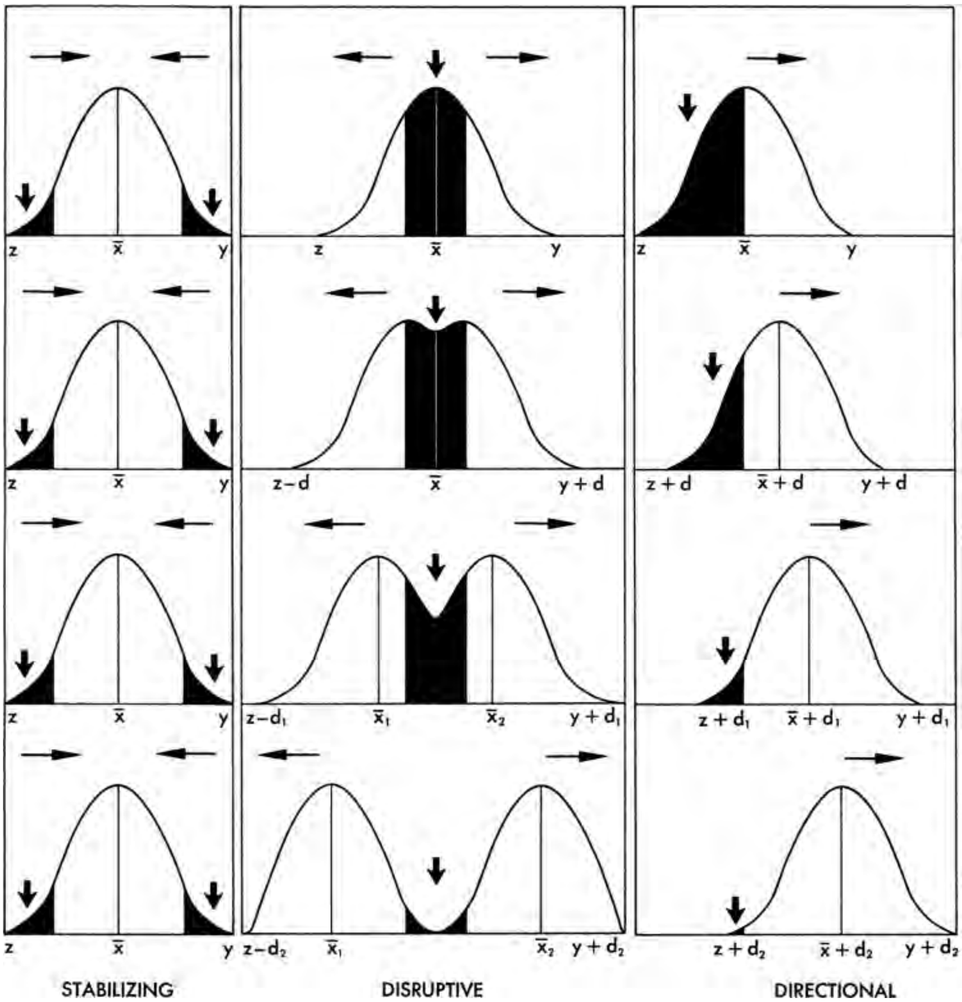

Figure 1.3 Three different effects of natural selection acting on a population. In each example, the x-axis is the ordering from low to high of some phenotypic trait, and the y-axis is the frequency of the trait. Stabilizing selection is selection that acts on both tails of the distribution and maintains the mean characteristic. In disruptive selection, the mean phenotype is selected against that resulting over time in two separate populations with different mean characteristics. In directional selection, the effect is on one of the tails of the distribution, which results in a shift in the mean characteristic. (From Solbrig OT. *Principles and Methods of Plant Biosystematics*, 1st edition, ©1970. Reprinted by permission of Pearson Education, Inc., Upper Saddle River, NJ.)

Futuyma (1998) points out that fitness is most easily conceptualized for an asexual organism in which all individuals reproduce at the same time and then die. There are no overlapping generations. A more extensive discussion of fitness is provided by Futuyma (1998).

Evolutionary biology mostly has been restricted to academia. Application of evolutionary thinking has been applied to agriculture (both crops and animals) and to some extent in disease control. However, applied evolution (Bull and Wichman, 2001) is being used in a variety of contexts including design of biotechnology protocols that result in new drugs and industrially important enzymes, development of computer technologies, and the avoidance of resistant microbes and pests.

Evolutionary Ecology

The study of organismal variability is the purview of evolution. Evolution is change. However, this definition is much too broad. Biological evolution involves the modification and diversification of organisms over generations. Evolutionary thought and studies have prevailed since Darwin opened the window and exposed a process that seems to explain much of biology. Over the past century, enormous strides have been made in our understanding of the theoretical and empirical processes that drive evolution. The discovery of DNA and genes and the development of molecular biology have opened up previously unknown processes, expanding our understanding of how evolution operates. However, it has become clear that evolution alone is not sufficient to understanding much of the pattern seen in nature. Ecology and evolution became united in the subdiscipline of evolutionary ecology, which sought to understand how evolution affects the ecology and how ecology affects the evolution of organisms. Much insight into the biology of many organisms has been obtained because of the union of these two disciplines.

Microbiology has been, in general, a science outside of both evolution and ecology even though many important observations that have advanced evolution have come from microbiology (e.g., *transformation*) and lateral transfer of genetic information. In the 1960s, a few microbiologists began to leave the laboratory and sought to understand some of the incredible processes that were occurring in nature that seemed to be controlled by microbes. Microbial ecology became a discipline.

Many of the studies performed by microbial ecologists have been describing the distribution or prevalence of various types or strains of microorganisms in a variety of habitats. Some of these habitats included the mouth, digestive system, various plants, sewage, oceans, rivers, and extreme environments such as hot pools, deep ocean vents, and Antarctic ice. The ability to sample and then describe the microorganisms found requires careful planning and an understanding of the environmental conditions that maintain the health and survival of the organism.

Microbial ecology was strongly influenced by clinical and medical microbiology, which required that microbes be cultured to pure culture so that a name could be attached. Over and over, it has been shown that there are millions on millions of microbes in environmental samples, but only a few of these organisms can be made to grow on laboratory media. Clinical and medical microbiologists have been successful in identifying the causes of many microbiologically induced diseases. Treatments of these diseases required knowledge of the basic biology of these organisms and the discovery of various antimicrobials that were sometimes species specific. Unfortunately, most environmental microbes defied isolation.

Were the microbes that grew on laboratory media representative of all the other unculturable microbes or an exclusive subset? To answer questions like these, researchers had to know something about relatedness. Comparisons required some level of knowledge of differences or similarities. In medical microbiology, disease-causing organisms were grouped into divisions based on various phenotypic properties. Classification of microbes in medicine is essential for effective treatment, but what about environmental studies? Do we really need to know the phylogenies of the microbes taken from nature? Species designations have clearly defined meanings for higher organisms (discussed later). Microbes live life differently from higher organisms and so we ask do such designations have any meaning for microbes?

In 1953, Watson and Crick successfully described the double helix structure of one of the most important molecules—DNA. DNA and its related molecule RNA have been found in every living organism. There are no exceptions. Many wonderful experiments have shown that DNA is the molecule of inheritance. The early evolutionists were hampered in their quest for understanding by not knowing the fundamental units of inheritance (i.e., the gene). These scientists knew there had to be something physical that contained and transferred genetic information, but they did not know what that material was. Discovery that DNA was the information molecule has propelled biology through the last half of the past century and into this new century. Why did life select this molecule over other molecules to carry the information of life?

The molecules of life are important in any discussion of evolution and especially evolutionary ecology. The history of those molecules forms the basis of evolution. A basic understanding of those molecules is necessary if we desire to understand evolution and, more importantly, if we seek to understand evolutionary ecology. In many ways, microbial ecology is essentially gene ecology because of the high level of environmental responsiveness expressed by microbes and the fact that there is not much more to a microbe than a bag of genes and a few gene products. Life has surrounded microbes with a cell membrane and, in some cases, a cell wall to protect and facilitate the life of the microbe. However, the incredibly small size of most microbes puts them in constant interaction with their environment. Unlike many higher organisms that are able to moderate their internal and external environments, microbes are a product of their environment. Microbes can in some ways alter their environment and make it more suitable for growth; however, they are very responsive to changes in the physical conditions to which they are exposed.

A basic understanding of two concepts (i.e., the molecules of life and the species concept) is essential before we begin any discussion of microbial evolutionary ecology. A thorough discussion of both of these concepts would take volumes. However, we must cover the topics sufficiently to understand the theoretical and empirical data that are presented in much more detail later. Much of ecology and evolution is based on the species concept, and most of evolution is based on changes and modifications of the molecules of life. We begin with a discussion of the molecules of life and present some models on which of these molecules were most important to earth's earliest inhabitants. To understand natural selection and evolutionary change, a basic knowledge of possible and plausible scenarios concerning the origin of life is needed. However, these models of the origin of life are likely scenarios and are not definitive.

Because all meaningful discussions of evolutionary ecology are based on the concept of a species, we will spend some time describing the various species concept models and their misapplication to microbes. As with the origin of life models, the concept of a species is difficult to pin down, especially for microbes.

Our presentation of microbial ecology sometimes follows paths known to most microbiologists, but at other times, we will discuss theoretical and empirical evidence developed for higher organisms and seek to find whether the concepts and predictions are applicable to microorganisms. Sometimes, we will be successful in application of evolutionary ecology principles to microbes; at other times, it may seem that we are trying to force concepts on an unyielding subject. If the approach we are taking is successful in helping microbial ecology students to see the world differently and to ask questions differently results in greater insight into the workings of nature, our task has been worthwhile.