Introduction

Microbial ecosystems are as varied as any other Earth-supported ecosystem, with distinctive climates and habitats, providing niches for the colonization and succession of a diversity of microbes. Microbial ecosystems are often established as partnerships in association with eukaryotic organisms. The partnership is frequently called symbiosis.

Definitions

Symbiosis, the living together of dissimilar organisms as originally defined by Anton de Bary in 1879, encompasses: (1) commensalism – two organisms living together, with little benefit or detriment to themselves or each other; (2) mutualism – two organisms benefiting each other; and (3) parasitism (sometimes referred to as pathogenesis) – one organism benefiting at the expense of another (Figure 1). Many textbooks now define commensalism as a situation where one member benefits and the other is unaffected. Commensals belong to the Archaea, Eubacteria, or Eukaryota. This article concentrates on the Eubacteria because they are the most numerous and the most well known of the commensals. It also focuses on the resident or indigenous microbes rather than on the transient ones. Nevertheless, Eukaryota such as yeasts and other fungi as well as various protists are well-known inhabitants of both plant and animal surfaces. A few examples are presented.

Commensalism is much less studied than either mutualism or parasitism, most likely because very little seems to happen in contrast to mutualism and parasitism. However, this is an erroneous impression as we become more aware of the vast numbers and types of prokaryotic commensals that live in association with their eukaryotic hosts. Also, changes in the conditions of a commensal’s habitat or a move to a new niche may cause a formerly neutral microbe to become parasitic or mutualistic. For example, *Helicobacter pylori*, the causative agent of ulcers, exists as a commensal or a pathogen depending on its host. *Pseudomonas aeruginosa*, found in the anterior portion of the nose, is a serious pathogen in the lungs of cystic fibrosis patients and can cause infections in other tissues if it becomes internalized. Other commensals protect their symbiotic partner from parasites (thus acting as mutualists), either by their very presence, that is, occupying sites where parasites could attach, or through their metabolism, synthesizing vitamins, catabolizing complex polymers, or mediating developmental processes.

Both plants and animals establish interactions with commensal bacteria. Often, the interactions with plant and animal surfaces involve the formation of biofilms – a community of bacterial cells, frequently of different species, adherent to a surface and to each other, and enclosed in a self-produced polymeric matrix. Overall, more is known about interactions between commensals and animals, mainly because of the relationship to human health, but new and exciting discoveries have been uncovered for plant–commensal interactions.

Commensals in Plants

In the harsh and competitive terrestrial ecosystem, plants offer the microbe a nutrient-rich oasis to make a home. Commensals colonize any plant tissue – roots, seeds,
stems, leaves, flowers, and fruits, each presenting different challenges and rewards to the colonizing bacteria.

**The Spermosphere and the Rhizosphere**

A single gram of garden soil may contain $10^9$ bacteria, $10^7$ fungi, $10^3$ protozoa, $10^3$ algae, and a diverse array of small animals. Within the vast subterranean ecosystem, nowhere are organisms more numerous than in the soils surrounding a plant. As soon as a seed germinates, it exudes a variety of metabolites into the soil, creating a rich habitat around the seed called the spermosphere. Bacteria borne on the seed and those indigenous to the soil proliferate and thrive in the spermosphere.

As the plant develops, intense microbial activity occurs in the region surrounding the root, known as the rhizosphere. When discussing root function, emphasis is usually placed on nutrient uptake from the soil; however, roots also deposit nutrients into the soil—a function that is often overlooked. Forty to eighty percent of the carbon captured during photosynthesis is released from the roots in a process called rhizodeposition. Nutrients are deposited into the soil as (1) cells sloughed from the root cap, (2) lysates from dying cells, (3) gelatinous mucilage that helps aggregate soil particles, and (4) exudates. Exudates contain sugars, organic acids, amino acids, proteins, vitamins, phenolics, and flavonoids. One gram of root is estimated to release 50–100 mg of exudate, enough to support $2 \times 10^{10}$ bacteria. Not surprisingly, the rhizosphere contains 10–100 times more bacteria than bulk soil. Furthermore, the diversity of microbes found in the rhizosphere can be staggering. Analysis of 16S rRNA DNA sequences demonstrates that the bacterial composition of the rhizosphere differs significantly from bulk soil. Microbes aggregate in areas where rhizodeposition is plentiful—around the root cap, elongation zone, root hairs, and where lateral roots emerge (Figure 2).

Most rhizosphere bacteria are considered commensals. They thrive in the nutrient-rich habitat provided by the root, but neither benefit nor harm the plant. However, the distinction between commensals, mutualists, and parasites is often murky. For example, *Rhizobium* species are renowned for mutualism, providing fixed nitrogen to their legume partners, in exchange for carbohydrates. However, in the absence of a legume host, *Rhizobium* colonizes other plants as a commensal.

Successful colonization of roots requires that bacteria compete with other microbes for resources and space. By improving their competitive fitness, bacteria sometimes benefit the host plant. For example, the most successful colonists efficiently break down and utilize root-derived organic compounds, which cannot be used by plants for nutrition. By degrading those compounds to feed themselves, bacteria inadvertently provide the plant with usable forms of the nutrient. Some rhizosphere bacteria become successful colonists by secreting antibiotics that kill competitors. Often, this war between microbes does not significantly impact the plant. In some cases, antibiotic production plays an important role in plant defense. For example, *Pseudomonas* species produce antibiotics that suppress fungal infection of plants.

**The Phyllosphere**

The phyllosphere is the aerial region of the plant colonized by microbes; its colonists are often called epiphytes. Fungi, algae, protozoa, and nematodes inhabit the leaf and stem surfaces, but the most abundant epiphytes are bacteria (averaging $10^6$–$10^7$ cells cm$^{-2}$).

Perhaps the most famous of the eukaryotic commensals on plants are the wild or indigenous yeasts (species of *Hanseniaspora* (Kloeckera), *Metschnikowia*, and *Pichia*), often associated with the white, waxy coating or ‘bloom’ found on grape berries. These wild yeasts are thought to impart a spoiled taste to the wine when used for fermentation, and hence are replaced by cultured strains of *Saccharomyces cerevisiae*, which normally is estimated to be present on only 1 in 1000 berries.

The phyllosphere is considered to be a hostile environment due to rapid changes in temperature and humidity, limited nutrients, and solar irradiation. Yet, phyllosphere commensals have adapted to cope with these conditions. For example, many epiphytic bacteria are pigmented to
prevent ultraviolet (UV) damage, and microbial communities preferentially develop along veins, and around trichomes and stomata, where nutrients leak from the plant surface.

Phyllosphere research has mostly focused on understanding pathogenic bacteria. Considerably less is known about the nonpathogenic epiphytes, although commensals appear to play a role in limiting the population size of pathogens. Until recently, traditional culturing assessed the composition of the phyllosphere community, but not all organisms can be grown under laboratory conditions. Using a culture-independent approach, 16S rRNA DNA analyses identified many species that had never been seen before on plants, indicating that phyllosphere communities are more complex than previously thought.

Recently, the presence of human pathogens in the phyllosphere has been linked to outbreaks of food-borne illness. Surveys have identified enteric pathogens such as *Salmonella* and *Shigella* on produce. These organisms colonize the phyllosphere as commensals, but in humans, the same microbes can become parasitic.

### Commensals in Animals

It is said that the human body is made up of $10^{13}$ human cells and an order of magnitude more ($10^{14}$) bacteria. The total collection of microbes in the human body weighs in at about 1.25 kg. The vast majority of these bacteria are commensals, but some of them could be considered mutualists because they synthesize vitamins that help their host or they protect their host against pathogens in various ways. However, when the balance is perturbed, some commensals may become pathogenic as in the examples of nosocomial (hospital-acquired) infections or if the host is sick or immunocompromised.

The natural habitat of commensals in adult humans is essentially ubiquitous on or in the body—the skin, the oral cavity, the upper respiratory tract, the gastrointestinal (GI) tract, and the urogenital tract. Each of these habitats has a different population of bacteria and eukaryotic commensals that make up the microflora, with the numbers and types of species differing from ecosystem to ecosystem. For example, just a few microbes normally reside in lungs, eyes, or stomach, whereas numerous bacteria inhabit the mouth and the intestines. Also, each ecosystem exhibits different conditions to which the bacteria must adapt. Some areas such as the skin are as dry as a desert and acidic in pH, thus presenting significant challenges to resident microbes. Others such as the large intestine can be likened to a rain forest, with multiple microecosystems and a vast diversity of inhabitants.

### The Skin

The skin or integument is the largest organ of any animal, the average human body has almost $2 \, m^2$ of skin. Its function is to protect the delicate internal organs from injury, which could lead to infection or death. Up to 3 million microbes, both prokaryotic and eukaryotic, are estimated to exist on $1 \, cm^2$ of skin. The latter figure is an average value because few microbes are found on the legs and arms, but many are found in the hairy regions of the body, including the armpits and the groin, and also in the moist areas between the toes. The sites on the skin that bacteria prefer to colonize are hair follicles where their presence may create problems, such as acne. This is the same area where certain eukaryotic commensals, namely yeasts such as *Malassezia*, are also found. *Malassezia* species are detected on the skin of the vast majority of people, particularly once puberty is reached and the sebaceous glands become more active.

Hands generally have relatively few microbes present because they are dry, often colder than most body parts, and lack sebaceous glands. However, bacteria can be easily detected by culturing methods (Figure 3), stressing the importance of hand washing to reduce microbe numbers.

Most of the skin-associated bacteria are commensals in that no harm or benefit ensues from the interaction. However, an extremely thin line separates commensals from pathogens or mutualists. For example, of the bacteria, mostly Gram positives, which inhabit the skin, *Staphylococcus* species sometimes switch from a commensal

![Figure 3](image-url)
way of life to a pathogenic one. They may cause skin lesions, abscesses, boils, or even more serious infections. *Propionibacterium acnes*, an extremely common skin inhabitant, is a horrific infectious agent in catheters and other medical devices, where it forms biofilms that are resistant to antibiotics or other killing agents. Other common skin-inhabiting bacteria include the microaerophilic propionibacteria (*Propionibacterium acnes*), which colonize skin pores resulting in acne, various corynebacteria, which preferentially colonize aerobic sites on the skin, and species of *Micrococcus*, which are obligate aerobes.

**The Oral Cavity**

The mouth is one of the best-studied areas for commensal bacteria residence because of the regular influx of nutrients, presence of water and favorable pH, which provide numerous microniches that support bacterial growth. The mouth is also an excellent example of microbial succession over time. Newborns are bacteria free, but quickly obtain a microflora from passage through the birth canal, mother's skin (touching and during breast-feeding) and mouth (kissing), and from the environment. Many of these initial inhabitants are transient, but within a few months, streptococci and obligate anaerobes take residence. The upwelling of teeth at 6 months of age leads to a new set of microecosystems, including teeth enamel, which become colonized by *Streptococcus sanguis* and other bacteria.

Using culture-independent techniques based on 16S RNA DNA sequencing, 141 predominant species were identified in different microniches of healthy, adult human mouths. Sixty percent of these had not been identified previously by culturing methods. The most common divisions of bacteria in the oral cavity are the Firmicutes (low G+C Gram positives), the Actinobacteria (high G+C Gram positives), the Proteobacteria (Gram negatives), the Fusobacteria (anaerobic Gram negatives), and a division of bacteria where none has been cultured. The different ecosystems, tongue, palate, teeth, etc., have distinctive microbial profiles, but certain Firmicutes such as *Streptococcus mitis* are found at all sites.

A large number of bacterial species colonize teeth, where they establish a biofilm consortium, that is, dental plaque. The biofilm protects the attached bacteria from the severe mechanical disruption that occurs with chewing, swallowing, and movements of the tongue. Not surprisingly, the bacterial flora of a healthy mouth differs from a mouth with either dental caries or periodontal disease; the latter is a very serious infection of the gums. For example, *Streptococcus mutans* or *Treponema denticola*, a spirochete, are not detected in healthy mouths, but are found in caries and in gum disease.

**The Gut**

The adult human intestine houses up to 100 trillion microorganisms and the microbiome (the genes of the gut microbes) represented by these organisms outnumber the number of genes in the human genome by more than 100:1. It was long believed that *Escherichia coli* was a major inhabitant of the intestinal ecosystem. This conclusion was probably related to the fact that very few bacteria isolated from feces could grow on artificial culture media, whereas *E. coli* grew very well. Later on, techniques were developed to culture anaerobic bacteria, and the ratio between anaerobe and *E. coli* numbers was found to be about 1000:1. However, the most recent analyses based on metagenomics, which involves isolating DNA from a particular ecological niche and then using 16S RNA DNA sequences to establish identity and relationship, have resulted in an explosion of information about gut bacteria. Based on this type of study, some 7000 different types of bacteria are estimated to inhabit the human gut. The microbes in the human gut are dominated by two facultatively anaerobic or completely anaerobic divisions: the Cytophaga–Flavobacterium–Bacteroides (CFB) group and the Firmicutes (clostridia), whereas the Proteobacteria (*E. coli* and relatives) come in as a distant third.

Whether or not the gut bacteria are considered commensals or mutualists depends on how strictly the definitions are applied. Besides synthesizing vitamins, the bacteria in the human gut, like those in animal rumens or termite guts, break down plant polysaccharides into simple sugars that are utilized by their host. However, human gut bacteria cannot break down the larger and more complex plant polymers such as cellulose, which can be utilized by herbivores with a rumen, such as cattle, or by termites with a diverse gut flora. Complex carbohydrates pass through the human intestine relatively unaltered. Nevertheless, the efficiency of plant polysaccharide breakdown exhibited by human gut microbes is significant.

Gut bacteria also shape both the immune system and tissue and organ development. For reasons that are still not completely understood, indigenous microbes do not trigger a damaging inflammatory response in their host. Recognition occurs, but the host tolerates its indigenous microbes, which can also induce developmental processes in their hosts. For example, exposing germ-free mice to the common gut bacterium, *Bacteroides thetaiotaomicron*, brings about increased absorptive capacity of the intestine due to an induction of angiogenesis that results in enhanced blood supply.

We start our lives alone, as bacteria-free organisms. Passage through the birth canal, kisses and hugs from parents and relatives, and sucking mother’s milk exposes us to the organisms that will inhabit our mouth, our GI tracts, and our skin for the rest of our lives. We are one with our symbionts, and they with us.
Introduction

Communication is a social behavior that mediates fundamental aspects of animals’ lives. It is important during reproduction – playing a role in attracting another individual of the same species and coordinating mating, and extending to aspects of parental care. It is also important in many aspects of survival – from being alerted to the presence of predators by warning calls, through signaling prey defenses, to indicating food sources and defending them. Communication is also often conspicuous to the extent of being spectacular; examples are choruses of songbirds, cicadas, and frogs, and the coordinated displays of fireflies.

Communication is generally thought of as a characteristic of animals, but there are instances in which plants share features of animal communication. For example, the response of some plants to airborne chemicals indicating that a neighbor has been attacked has features in common with the warning or alarm calls of animals. However, as most information on communication comes from the animal kingdom, this article deals with animal communication. The article will begin by introducing key concepts in communication; it will then proceed to discuss the influence of physical and social environments on communication behavior, and it will end by looking at current issues linking behavior and ecology and will touch upon a role in applied ecology.

What Is Communication?

As we shall see below, defining communication is not straightforward and has been the subject of considerable debate. However, there are three readily identifiable components of communication: (1) the signal, (2) the signaler, and (3) the receiver.