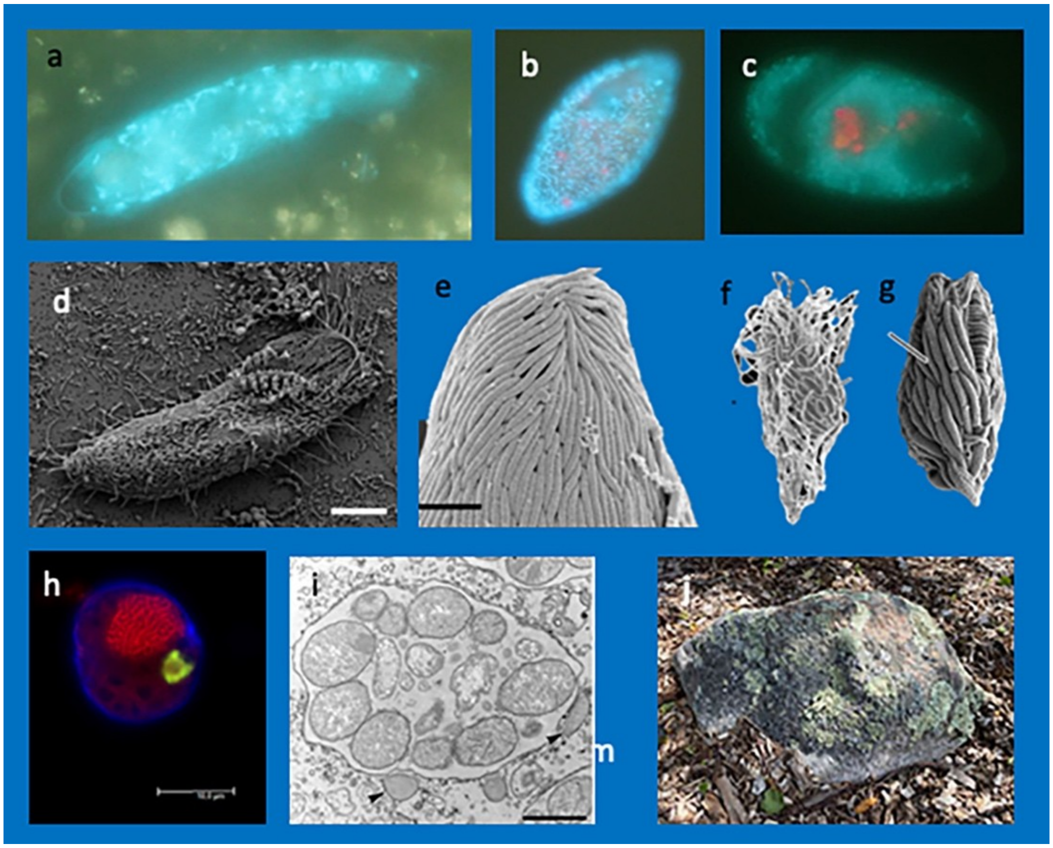
Symbioses

Someone told me that crusts on old stones are microbial partnerships: is this true?



Images of symbioses involving microorganisms. Panels a-d: freshwater and marine ciliates with fluorescently-labeled bacterial or archaeal symbionts (J. Rotterová, I. Čepička, and R. Beinart), e-scanning electron micrograph of surface of marine flagellate *Calkinsia aureus* with ectosymbionts (scale bar 300nm, N. Yubuki and B. Leander); f-g: marine ciliates with ectosymbionts from Cariaco Basin (W. Orsi); h: parasitic Syndiniales protist labelled with green fluorescence marker infecting a dinoflagellate host, host DNA labelled red (scale bar 10 µm, T. Sehein); i: transmission electron microscopy of internal membrane-bound compartment in a marine ciliate holding endosymbiotic bacteria (scale bar 0.5 µm, V. Edgcomb and J. Bernhard); j: a lichen on a rock (symbiosis between an alga or cyanobacterium and a fungus).

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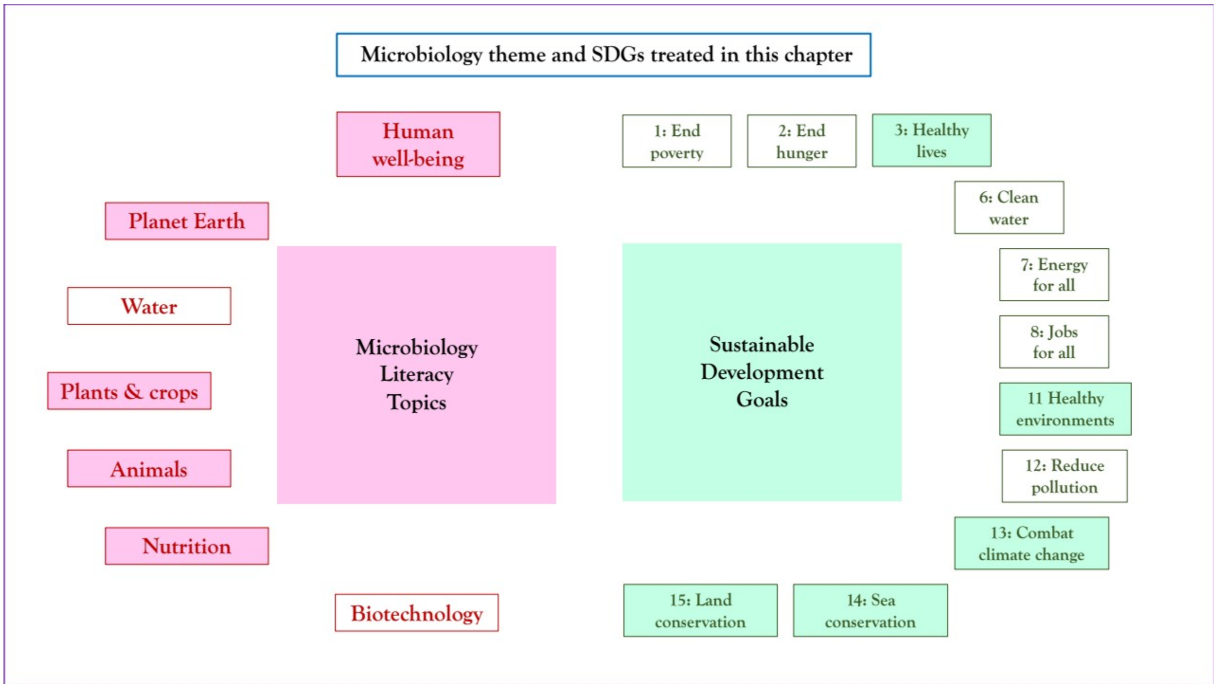
Storyline

Microorganisms (Bacteria, Archaea, protists, and microbial fungi) interact with each other and with plants and animals in relationships that we call **symbioses,** including those that form the crusts you see on stones and trees called **lichens**. Symbioses are interactions between two different organisms that live in close physical association with one another for the majority of their lives. A bird nesting in a tree, or a bee that visits a flower are not examples of symbioses because they spend much of their lives existing independently of one another. You may have seen pictures of a Clown Fish that lives within the tentacles of a sea anemone provided as an example of a symbiosis between two animals. Well, microorganisms form important symbioses as well. Some of these are beneficial to both partners, some are beneficial to only one, and others are beneficial to one, and harmful to the other. As you will learn, some are essential for the survival of the host! We still have much to learn about the majority of symbioses involving microorganisms, simply because so much of the microbial world is still being explored.

The Microbial and Societal Context

The microbiology: contributions to human and other animal health; plant and crop nutrition; essential for digestion of food for some animals; photosynthetic symbionts contribute to global photosynthesis and carbon and other nutrient cycling in aquatic and terrestrial ecosystems; participants in beneficial symbioses and causative agents in human (and other organism) disease.
Sustainability issues: health; food crop production; healthy environment; microbial symbionts can impact pools of climate-active gases; critical for survival of land and sea organisms.



Symbioses: the Microbiology

1. There are different types of symbioses. Some benefit both partners (mutualism), some benefit one partner but the other is not helped or harmed (commensalism), and some benefit one partner at the other's expense (parasitism). Occasionally, relationships between partners can change from one mode to another. Symbionts can live inside another species, in which case they are called *endosymbionts*, or on the surface of another species, in which case they are called *ectosymbionts*. Microorganisms participate in symbioses with all types of life, including other microorganisms.

2. ***Microorganisms have symbioses with other microorganisms***. Microorganisms participate in symbioses with other microorganisms (see images above). The microbial world is full of examples of symbioses where microbial partners cooperate to obtain essential molecules for life from their environment. These molecules include those that each can use for energy and for carbon. While our sources of carbon and energy are the cereal, milk, bacon and eggs that we may eat for breakfast, microorganisms use simple molecules such as sugars, carbon dioxide, amino acids, and even metals, just to name a few! Symbioses between protists and other microorganisms (Bacteria, Archaea and even other protists) are common, and serve a multitude of roles. Some symbionts are photosynthetic and can provide the host sugars made from photosynthesis. Some symbionts can fix nitrogen, which means they can convert the nitrogen in the air (nitrogen gas) to compounds (e.g., ammonia) that can be used by the host. Nitrogen is a nutrient that all living things require, and it is commonly in short supply. This is puzzling when you consider that ~70% of the gas in air is nitrogen! Yet this gaseous nitrogen cannot be used by most forms of life. Only nitrogen-fixing microorganisms can convert nitrogen gas into a form that can be used by other organisms. Microbial symbionts can carry out many processes involved in cycling of nitrogen, carbon, and other elements.

Animals and microorganisms form transient associations in nature routinely. Under certain conditions where there is an advantage to one or more of the partners to maintain this association, these transient associations can become stable symbioses over time when a microbial partner gradually loses its independence, or ability to survive outside of its host. This happens because some of the genetic material that is no longer needed by the symbiont (sometimes because the symbiont gets some of what it needs from its host) is lost, or is transferred to the genome of the host. The endosymbiont can be maintained to serve a limited function. This was the process that led to the acquisition of chloroplasts in early single-celled eukaryotes, the ancestors of land plants. Chloroplasts were acquired by early eukaryotes through the endosymbiotic acquisition of a photosynthetic cyanobacterium. Similarly, mitochondria (the organelles in cells of aerobic eukaryotes that produce ATP energy using glucose and oxygen) were acquired by early eukaryotes through symbioses with a bacterium. Symbiosis was the root of the evolution of photosynthesis in plants and aerobic respiration in animals.

Today, certain **mixotrophic** protists (those that have the ability to both eat and photosynthesize) that live in the sunlit water columns get their nutrition both by taking sugars from endosymbiotic photosynthetic algae or cyanobacteria *and* by consuming prey. Some bacterial symbionts of protists serve non-nutritional roles. For example, some are able to detoxify the host's immediate surroundings by removing toxic hydrogen sulfide. Other symbionts of protists that live in **anoxic** habitats are able to help the protist host's metabolism. For example, protists in anoxic habitats digest their food and produce their ATP energy through a process that does not require oxygen, called **fermentation**. But this process slows down if hydrogen produced by fermentation builds up. Some symbionts can take up this hydrogen for their own use, thus helping their host produce energy. There are symbioses between protists and bacteria that give **motility** to a non-motile host. Bacterial ectosymbionts on the cell surface of the protist host can move in synchrony, with the effect that they propel the host through its watery environment. Symbioses can even provide mechanical advantages. For instance, there is a marine protist that has bacterial ectosymbionts on its cell surface that contain iron-rich magnetic particles. The magnetic properties of those ectosymbionts help guide the protist host along Earth's geomagnetic field. This guidance helps to orient the protist toward the sediment surface on the seafloor where conditions are optimal for its survival. There are also symbiotic associations between different organisms based on cooperative metabolism. For example, plant sap-feeding insects host endosymbionts that utilize non-essential amino acids in the sap eaten by the host. These amino acids are vital for the microbial symbionts, which in turn, produce essential amino acids required by their eukaryotic hosts that are missing in their diet of sap.

3. ***Microorganisms are involved in symbioses with land plants.*** There are many bacteria and microbial fungi that live in association with plants and provide them important nutritional advantages that helps to produce healthier and more vigorous plants. For example, **Mycorrhizae** are microscopic **filamentous** fungi that live in symbiotic association with plant roots (e.g., with birch, willow, beech, pine, oak, spruce, and fir trees, orchids) increasing the surface area of the roots. This increased surface area allows them to take up more nutrients (nitrogen and phosphorus) and water from the soil. The fungi also increase plant's resistance to environmental stress and help it to hold the soil together. In turn, these fungi get **carbohydrates** from the plant for their food. So both benefit. There are also examples of

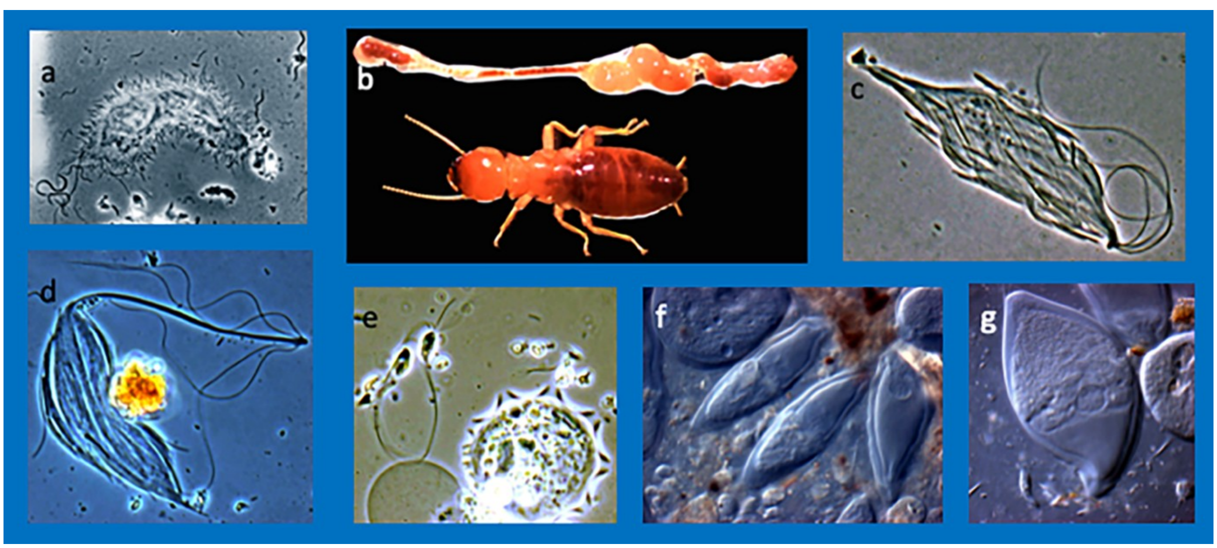
bacteria that live in association with plants that provide them with important nitrogen. For example, plants of the pea family, known as legumes are some of the plants that have bacteria (rhizobia) that live in small growths on the roots called nodules that carry out a process called **nitrogen fixation.** This is the process of converting nitrogen gas (most of what is in the air we breathe) to a form that can be absorbed and used by plants, ammonia. Plants can't do this conversion by themselves. The extra nitrogen provided by rhizobia provides increased nutrition for the plant, helping the plants grow and to protect the plants from disease.

4. ***Microbial fungi are involved in symbioses with algae and/or cyanobacteria, forming lichens.*** You probably noticed crusty growth on tree trunks, rocks, buildings, and other surfaces (panel j in image collage above, and below). This growth is likely mutualistic, since both partners benefit. The lichen can produce its own food because the algal (green algae or yellow-green algae) or cyanobacterial partner(s) is photosynthetic, and converts carbon dioxide to sugars using water and sunlight. The fungus obtains sugars from its algal partner and the fungal filaments provide a substrate for the alga and/or cyanobacteria to grow. The fungal partner also traps moisture and nutrients from the environment, and usually anchors the partnership to the substrate it is growing on (the tree, stone, etc.). The effects of lichens on trees is thought to be minimal, in fact nutrients from the lichens can be helpful to the tree when those are washed down the trunk during a rainstorm, to the roots. There are tens of thousands of lichen species worldwide.

Lichen (*Hypogymnia*) growing on a tree. *Hypogymnia* is genus of foliose lichens.

5. ***Humans have microbial symbionts!*** Humans (and other animals) have at least as many microorganisms living in our body as there are human cells! Most of these are bacteria that are mutually beneficial to both host (us) and the bacteria and live in our digestive tract and on our skin. They promote the development of a healthy immune system by communicating with, and exchanging small molecules with our immune system cells, thus preventing **pathogens** in our gut or on our skin from causing infection and illness. The human gastrointestinal tract offers nutrients and protection to the microorganisms that live there. In turn, many of these microorganisms complete important functions for the host, including breakdown of fiber and production of vitamins such as A, B2, B3, B5, B12, C, D and K. Having a healthy gut and skin community of microbial symbionts can also help protect the host (you) from pathogenic microorganisms by consuming nutrients required for pathogen survival, and secreting toxins and anti-microbial compounds that inhibit growth of pathogens. For example, *Staphylococcus epidermidis*, which lives on skin all over our body, produces antimicrobial proteins that help our immune system. There are protozoan parasites, such as *Giardia lamblia*, that can enter the human gut from contaminated water and can cause disease. All animals have microbial symbionts in their guts.

6. ***Microbial symbionts of termites and ruminants provide 100% of the nutritional needs of those animals!*** Endosymbionts that live within the intestines of termites help to convert the wood that the termites eat into nutrients that the termite is able to digest. Without these symbionts, the termite would not be able to get nutrition from the wood it ingests. This is a mutualism because the protozoa, bacteria and archaea that live within the termite gut benefit also by getting a constant supply of food (wood) from the termite. The protozoa in the termite gut secrete the enzyme cellulase, which breaks down the lignocellulose in the wood into sugars that the termite can absorb through their digestive tract. Digestion of lignocellulose by termites is actually a series of activities carried out by the host termite and its gut microbiota. The end products include acetate and variable amounts of methane and hydrogen. Methane is a greenhouse gas, so yes, termites "fart" methane gas and contribute to greenhouse gas production. Many termites have microbiota that includes protists, bacteria and archaea, but some lineages lack protozoa. Termites also use other nutrients produced by their endosymbionts. Other protists, bacteria, and archaea are symbionts of some insects. Aphids and tsetse rely on nutritional support from their bacterial endosymbionts.



Examples of symbiotic protists associated with the hindguts of wood-feeding, "lower" termites. The hindguts of any species of so called "lower" termites contain a diverse microbiota, representing all three domains of life: hundreds of species of diverse Bacteria, several species methanogenic Archaea, and up two a dozen species of anaerobic, mitochondrion-less protists (Eucarya). Frequently, symbioses within symbioses may be observed, with specific bacteria and archaea found as endo- and ecto-symbionts of specific protists. **a,** wave shaped bacteria known as spirochetes can be observed attached to the surface of a protist belonging to the genus *Pyrsonympha* in the hindguts of the termite *Reticulitermes flavipes*. **b,** A "worker" nymph of the dampwood termite *Zootermopsis nevadensis* (lower), along with a gut tract extracted from a separate worker (upper). The majority of the symbionts are located within the bulbous hindgut paunch (upper left). Examples of hindgut protists from *Zootermopsis nevadensis* include: *Streblomastix strix* (**c** & **d**), a thin oxymonad itself covered with a coat of long, thin bacteria belonging to the phylum Bacteroidetes; in **d,** the central protist has become separated from its coat of bacteria. **e,** methanogenic archaea (not shown) are often found associated as endosymbionts of two other protist species from *Z. nevadensis*; the smaller *Trichomitus* sp. (upper left) and *Trichomitopsis termopsidis* (lower right), which has been unequivocally been demonstrated to be cellulose fermenting. **f, g,** Cellulose decomposing *Trichonympha* sp., also from *Z. nevadensis*, have been demonstrated to host multiple endo- and ecto-symbiotic bacterial species (not shown). Credits: Jared R. Leadbetter, Caltech.

7. ***Ruminants (cows, goats, sheep, horses, etc.) that eat grass and other plant material exclusively, also require microbial symbionts to digest the cellulose in that plant material.*** The first stomach of a ruminant is called the *rumen*, which receives the food or cud, partially digests it with the aid of microorganisms, and passes this mixture on to the rest of the digestive tract. The endosymbionts of ruminants include bacteria, protozoa, fungi, archaea and viruses. The exact community inside the rumen depends on the plant food the animal is eating. Cellulose is the main organic compound in the cell walls of plants. Without these mutualistic symbionts, ruminants would not be able to effectively obtain nutrition from the lignin, hemicellulose or cellulose in plant material. The digestive activities of the microorganisms in the rumen enable the animal to obtain protein and fatty acids from the plants that they eat. In turn, the ruminant animal chews the plant material into small pieces that help the microorganisms break it down, and the animal provides water, warmth, and anaerobic conditions in the rumen that the microbes require for **fermentation** of the plant material. A by-product of fermentation in the rumen is gas that is approximately 60% carbon dioxide and 40% methane, greenhouse gases. An adult cow can produce as much as 50 liters of gas per hour!

8. ***Some symbioses between microorganisms and humans are not good for human health***. Some microorganisms form parasitic symbiotic relationships with human cells, and these parasites make us sick. For instance, *Giardia* and *Cryptosporidium* are protozoan parasites that causes diarrheal illness in humans. They can be found on surfaces or in soil, food, or water that is contaminated from feces (poop) from infected humans or other animals. Other protist examples include the parasite *Leishmania* and the parasite *Trypanosoma* that are both spread by the bite of certain types of sandflies (e.g., tsetse flies). *Leishmania* causes skin ulcers in humans, canids (dogs) and rodents, and Trypanosoma causes "sleeping sickness." The former is found in parts of the tropics, subtropics, and southern Europe, and the latter, is only found in sub-Saharan Africa (see topic on protists for more examples of protist pathogens).

Relevance for Sustainable Development Goals and Grand Challenges

Microbial symbioses are relevant to several SDGs (microbial aspects in italics), including

- **Goal 3. Microbial symbioses with beneficial microbes are critical to the health of humans (and other animals), but certain protist parasites can cause disease** *(provide critical digestive/ nutritional support, some have negative effects on human health in certain parts of the world)* Scientists have become aware that the "human **microbiome**" consists of many different types of (predominantly) bacteria that live in the human intestines that are critical for maintaining healthy bowel function and that help us obtain nutrition from our food. When we take **antibiotics** for colds and various other infections, these can not only kill the bacteria in our bodies that are making us sick, but they can kill the "good guys" in our intestines. This is why doctors often recommend that we eat yogurt and other "**probiotics**" that help us to repopulate our guts with friendly microbes that we need. There can also be unfriendly microorganisms in animal guts that can infect other animals (including humans) that come into contact with them through food or water that is contaminated with feces. Freshwater is a precious and limited resource for all life on Earth. Preserving clean water for drinking and recreation by not wasting fresh water), as well as practicing good personal hygiene (washing hands, disposing of human and animal waste properly) is critically important in order to preserve this finite resource. In parts of the world humans do not have adequate access to drinking water, let alone clean drinking water, and this is creating a humanitarian crisis. Think about this when you turn on the faucet for washing your dishes or car, bathing, or for recreation. Don't leave the hose or faucet running when it is not needed, and eliminate wasteful and unnecessary habits. Consider only growing plants around your home that can survive on the amount of water they naturally receive through rainfall in the climate where you live.
- **Goal 11: Symbioses involving microorganisms are characteristic of healthy environments** *(healthy environments have plenty of biological diversity, and this includes symbioses)*. When microorganisms establish different symbiotic associations with other microorganisms or with plants, fungi, and animals, this helps them survive in a wider range of possible habitats because these associations expand their metabolic repertoire. For example, the gammaproteobacterial symbionts that live in the gills of shipworms help them to digest cellulose, and hence live on, and digest sunken wood on the ocean floor. Most bivalves that occupy **hydrothermal vents** on the seafloor, such as the giant mussel *Bathymodiolus* also have bacterial gill-associated symbionts that **oxidize** sulfur and methane which sustains host nutrition and growth. Bacterial plant root symbionts support the nutritional needs of the plant and help that plant grow in habitats that otherwise would not provide adequate nutrition.
- **Goal 13: *Symbionts in the guts of many animals contribute to greenhouse gas production*** *(animal food production needs to take into account the environmental cost of growing that animal. This includes its water consumption, grazing impacts, and the production of greenhouse gases by the microorganism that live it its gut)*. Animals commonly have symbionts in their digestive tract that produce carbon dioxide (CO_2) and methane (CH_4) as a by-product of their metabolism. This is particularly true of ruminants (e.g., cows) and termites, which burp and fart CH_4, a potent greenhouse gas, into the atmosphere. This CH_4 (as well as CO_2, another less potent greenhouse gas) are produced by gut microbial symbionts as they break down plant material ingested by the animal. About 40% of the

annual inputs of methane into the atmosphere are from grazing animals grown for human food, and that number is growing each year as demand for meat and dairy increases. Give this some thought when considering whether it is more sustainable to grow animals or plants for feeding the human population.

- **Goal 14: Sea conservation** *(pollutants decrease biological diversity)* Water pollution kills not only animals and plants that live in the water but also some fraction of the microbial population. This can eliminate microorganisms that play critical roles as symbionts of animals. When those symbionts are lost, the animal dies. As the world warms (on average), sea temperatures rise. This is also having a negative effect on ocean health because increasing temperatures stress plants and animals. Some animals cannot cope with temperature increases of only a few degrees. For example, corals are marine **invertebrates** (phylum Cnidaria) that have an **obligate symbiosis** with dinoflagellate protists that are very sensitive to increases in temperature. Corals typically live in clear waters that are nutrient poor, and they do not have the resources to produce their own energy. Instead, they rely on their photosynthetic, microalgal protist symbionts (zooxanthellae) for energy. The coral consumes the sugars released from their dinoflagellate symbionts and releases carbon dioxide and **inorganic nutrients** back to their photosynthetic partners. Coral "bleaching" happens when waters get too warm, causing the coral to expel the zooxanthellae, and turning the empty coral skeleton white. These corals can survive such bleaching events, but they stress the coral and repeated events can be fatal.
- **Goal 15: Land conservation** *(Industrial agriculture practices can lower biological diversity and can eliminate important soil microorganisms that play roles in beneficial symbioses with plants)* Farming practices that include application of strong pesticides and herbicides, frequent tilling, and irrigation, can destroy soil microbes involved in nutritional symbioses with the roots of plants, and/or destroy the soil fabric, making it hard for them to survive. Clearing landscapes of trees and other vegetation for construction projects can have similar effects.

Potential Implications for Decisions

1. ***Individual***

   a. Should I drink this water in this stream that looks clear? I'm really thirsty!

   b. Do I think that farmers worldwide should be growing more animals or plants to feed the human population? Does my answer change my thinking about what my personal consumption habits should be?

   c. Does the fast-food industry contribute to greenhouse gas production?

   d. When the doctor tells me to take antibiotics, why should I consider eating yogurt with live cultures?

   e. Are there beneficial microorganisms that live on my skin?

2. ***Community policies***

a. What are the local public health consequences of letting animal waste (human or from pets or livestock) come into contact with water bodies used for drinking water or recreation?

b. How can application of pesticides and herbicides affect the health of the plants I grow? How can addition of compost help?

c. Can we be more sustainable as a community in terms of preserving precious freshwater resources by discouraging people from growing certain plants on their property that require watering because rainfall where we live does not provide enough water naturally for their growth (e.g., grass lawns, tropical plants)?

3. National policies relating to water and air quality, hazardous waste disposal

a. What kinds of laws should be enacted to limit the damages caused by livestock grazing?

b. Should greater resources be directed toward growing plant or animals for food as a nation and why?

c. What changes can be made to reduce pollution of water bodies (rivers, streams, lakes, ponds, coastal areas)?

d. Is there such thing as "too clean" of an environment?

Pupil Participation

1. Class discussion about symbioses involving microorganisms, giving examples involving all major groups of plants and animals

2. Student awareness about symbioses involving microorganisms

a. There are protist parasites of humans. Give examples and discuss where they would be found and how they are transmitted

b. Discuss what ruminants are, what they eat, and the fact that they rely on their gut symbionts to help them digest the plant material they eat.

c. Discuss climate change, including global warming of waters (on average) and how that leads to loss of critical coral symbionts (bleaching). Discuss what happens to the reef ecosystem when/if the corals die.

d. If you were in charge of feeding the world would you grow more grains or would you grow more meat and why? Should developed countries lead by example on this or should your instructions only apply to rapidly developing countries with large populations and why?

e. What are the impacts on the environment of the fast-food (burger) industry?

The Evidence Base, Further Reading and Teaching Aids

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Glossary

Anaerobic-without oxygen, an organism that grows without oxygen.
Anoxic-an environment without oxygen.
Antibiotics-compounds in certain medicines that help stop infections caused by bacteria by killing them or keeping them from reproducing. They are naturally produced by microorganisms for conducting chemical warfare on eachother, and some are useful for human medicine.
Carbohydrates-molecules made of carbon, hydrogen, and oxygen, with a ratio of hydrogen to oxygen of 2:1, including sugars, starches, and fibers found in fruits, grains, vegetables, and milk products.
Fermentation-a metabolic process that converts organic compounds, carbohydrates, into an alcohol or an acid to obtain energy
Filamentous-thin in diameter, resembling a thread.
Inorganic nutrients-nutrients not containing carbon
Invertebrates-animals lacking a backbone
Micorrhizae-filamentous fungi that live in association with plant roots and enhance their ability to uptake nitrogen and phosphorus by increasing the surface area associated with the plant root, allowing the plant to more reach nutrients and water.
Microbiome-all microorganisms (bacteria, fungi, protozoa, archaea) and viruses that live on and inside the body.

Motility-the ability of an organism to move independently using metabolic energy.
Nitrogen fixation-the chemical process whereby atmospheric nitrogen (N_2) is converted into ammonia (NH_3) or other nitrogen-containing compounds.
Obligate symbiosis-one or both partners are entirely dependent on each other for survival
Probiotics-living microorganisms that when consumed are thought to improve health by restoring the natural flora of your gut.
Symbiosis-a relationship between 2 different species that live in close association with one another for the majority of their life cycle. This relationship can be beneficial or not.
Lichen-comprised of a fungus living in symbiosis with an alga or cyanobacterium (or both in some cases).