Termites and their microbes

Miss: last night I saw on TV enormous 4000 year-old termite mounds in Brazil that could be seen from satellites. But what do termites do?

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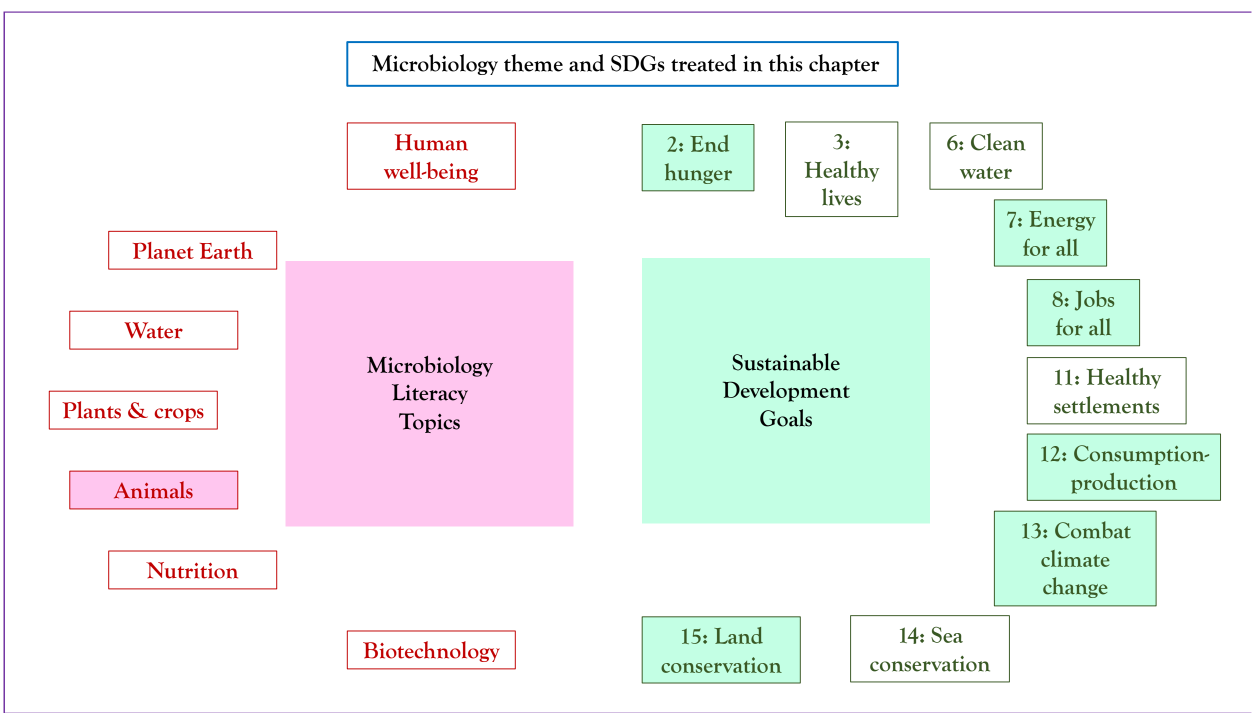
Termites

Storyline

Although certain species of termites are important urban pests responsible for massive damage to wooden structures globally, these constitute less than 5% of the over 2000 species of termites. They cannot tell the difference between wood in a forest or the wood in your house! The vast majority of termite species provide valuable ecosystem services, particularly through the recycling of wood, grass, and leaf litter. However, this is sometimes accompanied by the release of methane — an important greenhouse gas. The termite diet is composed of a substance called lignocellulose, which is very hard to digest, and contains very little nitrogen, an essential element in all living things. Termites therefore rely on dense microbial communities in their digestive tracts, called gut microbiomes, to break down lignocellulose and supplement their diets with "fixed" nitrogen. Understanding the process of symbiotic digestion in termites is central to understanding their role in the environment, may also hold the key also to the production of eco-friendly biofuels from plant waste, and help regulate greenhouse gas emissions from termites as well as other animals.

The Microbiology and Societal Context

The microbiology: the termite microbiome and wood digestion; ecosystem engineers; economic impact as wood-destroying pests; climate change and the spread of invasive termite species; potential sources of biofuels. *Sustainability issues*: potential use for biofuel development; termites as structural, agricultural, and forestry pests; dead wood recycling/composting; nitrogen fixation; greenhouse gas emissions; biodiversity.



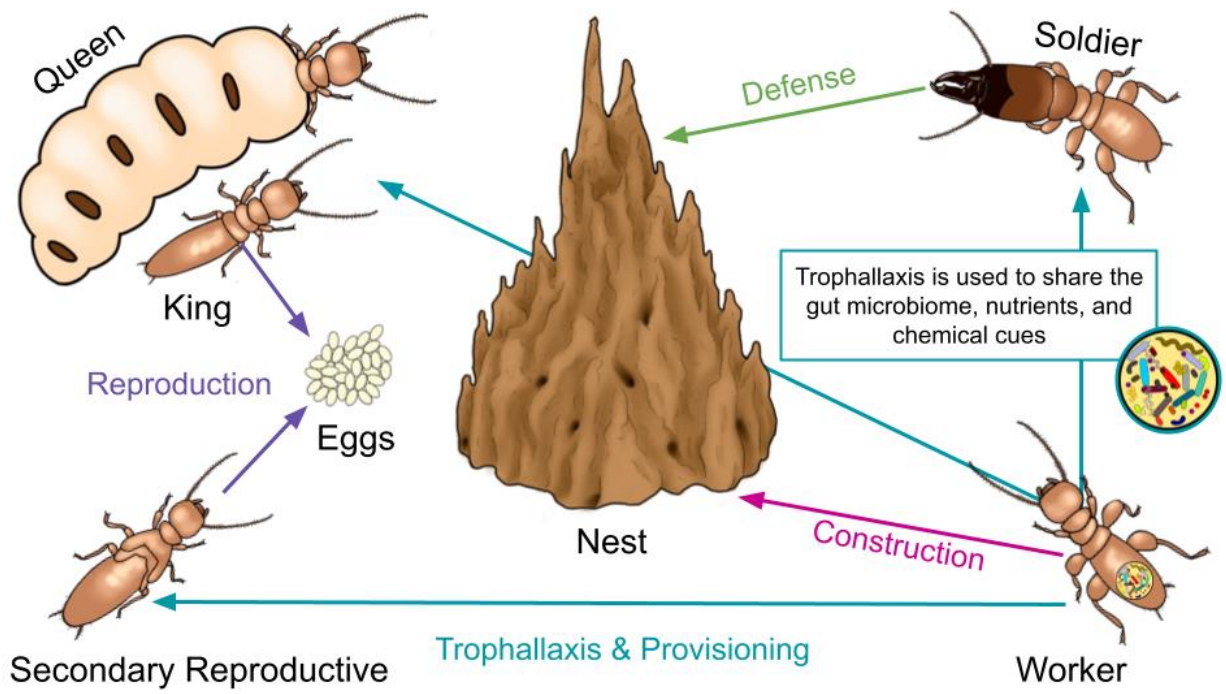
Termites: The Microbiology

1. Symbiotic digestion in termites. Termites typically feed on dead plant material which is generally hard to digest for animals and lacks basic nourishment. The termites overcome their dietary challenges with the assistance of collections of microbial symbionts in their guts called "gut microbiomes." Termite microbiomes may include bacteria, archaea, or protozoa, and they aid in the digestion of lignocellulose, the major structural component of plant material. Based on the presence or absence of protozoan symbionts in their guts, termites can be grouped into lower (protozoa-harboring) and higher (protozoa-free) termites - both groups however have bacterial and archaeal symbionts.

2. Termite gut microbiomes and nitrogen fixation. Apart from helping termites overcome the difficulty of digesting their diets, their microbiomes also provide them with nitrogen, N, — an element required by all animals to make amino acids, proteins, and DNA. Biological "N_2 fixation" is a critical process through which bacteria convert atmospheric nitrogen, which cannot readily be used by most forms of life, into more usable forms, like ammonia (NH_3), and many symbiotic bacteria in termite gut microbiomes have been known to do this. Because wood is very poor in nitrogen, the ability of the gut symbionts to fix N_2 is critical for termite nutrition.

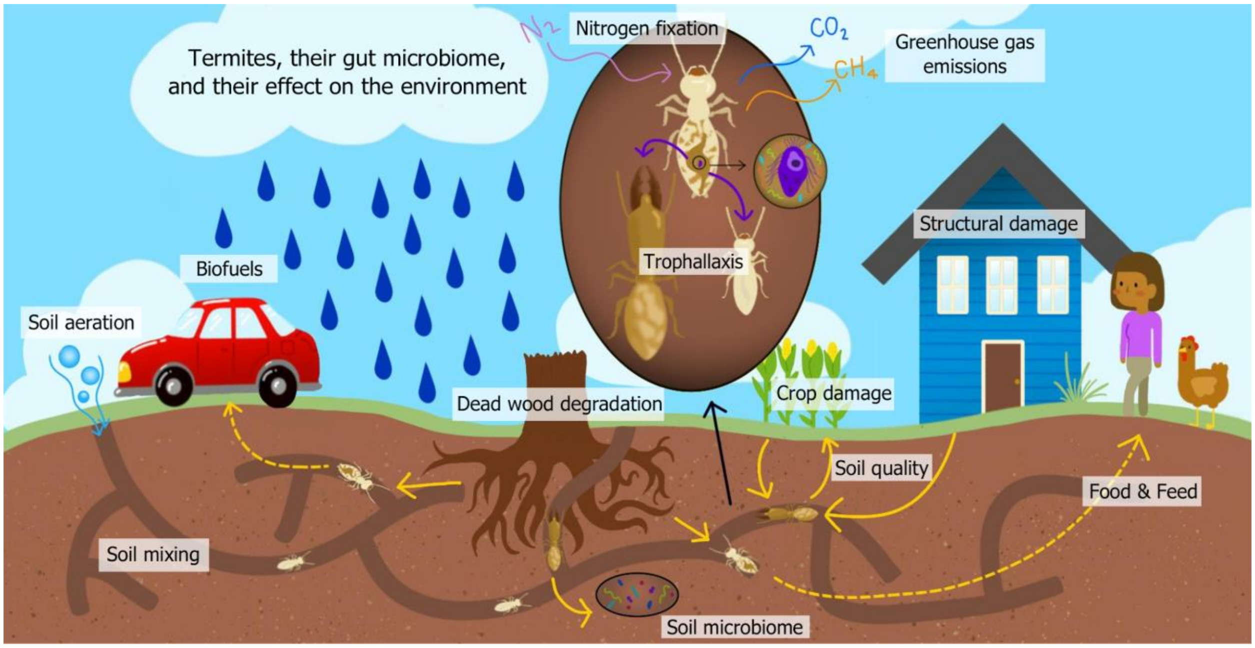
3. Eusociality and trophallaxis. Termites are eusocial insects, meaning that they live in large (made up of up to a million individuals) multigenerational family groups called colonies and demonstrate an extreme division of labor, or role specialisation. Most individuals in a colony have given up their ability to reproduce to a few reproductive nest-mates. These reproductive individuals are the queen and king, as well as some "secondary reproductives" that can also lay eggs. Generally speaking, the worker caste is responsible for maintaining the nest and represents the primary consumers of plant material, while the soldiers are responsible for protecting the colony from invaders and predators. The workers engage in trophallaxis, an important behavior that enables the feeding of dependent castes like soldiers and younger termites who cannot effectively feed on the plant material themselves. Trophallaxis enables the exchange of information, nutrients, and most importantly gut symbionts. The symbiotic system of digestion combined with trophallaxis and extreme task-specialization makes a termite colony a highly efficient wood-digesting "machine."

4. Termites are ecosystem engineers. Thanks to their fiber-digesting symbionts, termites are the most critical decomposers of plant material in tropical and subtropical forests, making them crucial to the functioning of the carbon cycle. Also, because of their symbionts' ability to fix nitrogen, and because they form a significant portion of the protein-rich diets of many animals, including aardwolves, numbats, and bat-eared foxes, termites are also central to nitrogen cycling in these ecosystems. Much like earthworms, termites play a significant role in loosening, aerating and mixing soil. The accumulation of resources in termite nests results in them being important reservoirs for nutrients, supporting the growth of plants around the nest. Termite nests are also home to a host of other insects, either living alongside them, or moving into nests after the termites are done with it. Other animals which use termite nests or mounds after the termites have left include vertebrates, like reptiles, birds, and some small mammals. Reptiles use mounds as basking spots, birds use them as perches, and both groups have been known to use the mounds as incubators for their eggs.



5. Termites cause billions of dollars in structural, agricultural, and forestry damage each year by eating wooden structures. The gut symbionts that have helped termites become ecologically successful as degraders of wood and other forms of plant material are also responsible for their success as structural pests. While they are relatively small animals on the individual level, large colonies of wood-feeding termites can eat around 5 kilograms of wood per month. Their voracious appetite for wood results in tens of billions of dollars of damage per year in wooden structures and forests. Termites have also been found to cause significant damage to living plant material such as: sugarcane, palms, fruit trees, rice, maize, wheat, sorghum, cotton, peanuts, eucalyptus, cassava, coffee, soybeans, and more, including some vegetables. In some cases, termite pests have been known to cause total loss of crop yield, particularly in drier tropical regions. Termite control can be done through the use of chemical or biopesticides. Biopesticides are a popular alternative to the conventional chemical pest control methods, as they typically act on a specific target species, and are not as prone to causing environmental pollution which could affect other animals, including humans, as well as soil and water quality.

6. Climate change and invasive species. Climate change can significantly impact the distribution and spread of species on the planet. An unfortunate byproduct of lignocellulose degradation is the production of methane, an important greenhouse gas. Because termites are eusocial and live in large groups of individuals that are all fermenting plant materials in their guts, the contribution of termites to the greenhouse effect is significant, making about 3–4% to the global methane and 10% of the CO_2 budgets. Although termites may be important contributors to the global greenhouse gas budget, human activities, such as the burning of fossil fuels, have had a far more rapid and large-scale impact through the breakdown of ecosystem services and the loss of biodiversity. As a result, termites are also affected by climate change, which has led to the spread of invasive species, including termites, to warmer regions where they may outcompete local insect groups and potentially act as structural pests. There is also evidence that higher temperatures can lead to hybridization between invasive termite species to produce robust hybrids that can further disturb the ecological balance or act as even more problematic pests.



*7. **Termites may help with the future production of biofuels.*** Our demand for the very limited petroleum resources is ever-increasing and planning for a smooth transition to renewable biofuels is in the long-term interest of humanity and the planet. Over millions of years of evolution, termites have evolved to be highly specialized bioreactors that can convert biomass to products, such as hydrogen (H_2) and methane that have value as renewable sources of energy. It has been estimated that 10,000 termites can produce as much as 87-94 liters of H_2 every day! H_2 as a biofuel produces no greenhouse gas emissions, is light-weight and longer-lasting than batteries; it is so effective that it has even been used to fuel spacecraft. If the conditions of the termite hindgut can be recreated on a large scale, we could have an efficient method of converting lignocellulose into usable energy, such as H_2, which is currently being produced mainly from non-renewable resources.

*8. **Termites hold promise as a food source for humans and livestock.*** As previously mentioned, termites are major protein-rich components of the diets of predators, from ants to aardvarks, in tropical and subtropical forests. Insects have been farmed as "mini-livestock" for decades as better sources of protein for humans and livestock than many plant- and animal-based sources. However, termites may have an advantage over traditionally farmed insects, like crickets, which require protein- and nutrient-rich diets in order to be nutritious food sources themselves, because their gut microbiome allows them to thrive on food sources with much lower nutritional value than other insects. Termites are already used as poultry feed in Guinea, Togo, Burkina Faso, and India, and are likely to grow into a popular alternative for other countries, not only for consumption by livestock and poultry, but for humans as well. In fact, winged reproductive termites are commonly harvested and eaten during their swarming seasons in some countries.

9. Biodiversity. There are about 2,000 known species of termites in the world, and some scientists believe that there may be many more termite species that have not been described yet. Termites directly contribute to the biodiversity of their environment by just existing but, as important members of food webs, they also support the diversity of other forms of life. As previously mentioned, they are eaten by many different animals, including humans, and they even protect the environment, by providing ecosystem services. Termites carry within them many different kinds of protists and bacteria, some of which do not exist anywhere in the world outside of the termite gut! If termites were to go extinct, we would also lose these unique microorganisms. With the introduction of new invasive termite species, native termites are forced to compete or even possibly interbreed with other termites never before encountered. This increases the success of the invasive species, which may overtake native termite species and cause a ripple effect on other animals that interact with the native termite species, having an overall negative effect on biodiversity.

Relevance for Sustainable Development Goals and Grand Challenges

- **Goal 2: End hunger, achieve food security and improved nutrition and promote sustainable agriculture:** Termites have been part of the human diet since prehistoric times, and are still being eaten by people today. They are also used as feed for livestock and poultry in several countries. As climate change pressures people to choose more sustainable diets, replacing some animal-based proteins with termite proteins will be an efficient way to convert otherwise indigestible plant-based waste into protein.
- **Goal 7: Energy for all:** The efficient digestion of lignocellulose by the microbes in the termite gut may prove useful in the development of a future biofuel from plant-based waste. Although replicating the conditions of the termite hindgut may not be feasible with current technology, it may become easier with further developments in biofuel production.
- **Goal 8: Jobs for all:** The massive amount of damage that some termite species cause as structural and agricultural pests provides job opportunities to pest management professionals as well as the pesticide industry and many scientific researchers hoping to solve the termite problem. Additionally, the development of a biopesticide that is effective against pest insects, including termites, is important to avoid unintended negative consequences of spraying chemical pesticides, like soil and water pollution and the products and chemicals used in the production of the pesticide itself. Developing a biopesticide product for termite control will require a lot of research and the work of hundreds of people in research institutions and within the pesticide industry and the government. The production of biofuel using termite-derived technology will also involve the work of countless people, from research and development scientists to business professionals and politicians. And, last but not least, by shortening the lifespan of construction timber, and hence timber-based structures, termites indirectly contribute to growth in the construction industry.

- **Goal 12: Sustainable consumption and production:** Termites have proven to be a critical part of the ecosystem. They degrade dead plant material, such as wood, which may not otherwise be as easily broken down without their presence. Not only do they serve as important composters/recyclers in the environment, they are also a food source for wild animals. Termites provide a number of ecosystem services, contributing to abiotic and biotic factors in their surrounding environments. Their nests provide shelter to other animals, increase soil nutrients, physically alter landscapes, and they are key players in the carbon and nitrogen cycles.
- **Goal 13: Combat climate change:** Termites do emit some greenhouse gases; however, massive livestock rearing operations contribute significantly more to methane emissions, contributing 37% of methane emissions resulting from human activity. Furthermore, about half of the methane produced by termites is then broken down by methanotrophic bacteria that live in their nests, reducing the amount of the greenhouse gas ultimately emitted from the colony. Slowing climate change would also help in slowing the spread of invasive termite species' geographical range, and reduce chances of hybridization between different termite species. Decreasing the intake of cattle protein and increasing termite protein in human and/or animal diets could also result in the release of less methane into the environment, utilizing a much smaller amount of land area to raise, and producing less methane overall while also recycling dead plant material.
- **Goal 15: Land conservation:** Land conservation allows for increased termite abundance and diversity, which in turn allows termites to make significant contributions to the health of the ecosystem. Destruction of land used by these important ecosystem engineers would result in a massive impact on the carbon and nitrogen cycles, termite predators, and the animals which live inside and around the nests and mounds of termites. Termites have also been found to protect rainforests from drought by increasing leaf litter decomposition, which helps to improve soil conditions that support tree growth, and extremely valuable component of rainforest conservation as the climate continues to change.

Potential Implications for Decisions

1. ***Individual decisions***
   a. Considering what to do in the case of a termite infestation at home: store-bought pesticides– what are the unintended consequences of chemical pesticides (pollution)? Were they produced sustainably? Would you prefer to use biopesticides?
   b. Personal convictions around eating termite (or insect)-derived protein or livestock fed on termite-derived protein vs eating conventional livestock.

2. ***Community policies***
   a. Considering the ecological benefits of having termites in your surrounding environment when using pesticides to treat termite infestations.
   b. Weighing the health, environmental, and economic benefits of wide-scale termite farming for poultry or human consumption against further environmental damage and higher cost (compared to raising livestock).

c. Cost associated with termite damage to buildings, effects of the infestation of one structure in a community on other structures around them.
d. Protection of local parks and other natural non-pest termite habitats; stricter policies on littering, pollution, and forestry practices.

3. National policies

a. Incentives for farmers to reduce their carbon footprint by using insect-based proteins and approval of termites by governments as food for humans and feed for livestock, aquaculture, and poultry.
b. Approval of termite-targeting biopesticide products; switching to biopesticides will reduce the release of chemicals into the environment that could potentially harm beneficial organisms (microbes, plants, and animals).
c. Land conservation policies to protect non-pest termite species which provide important ecosystem services and serve as a food source for other animals.
d. Policies to prevent the introduction of invasive termite species– increasing quarantine times for (more in-depth government-supported screening processes of incoming shipments and luggage at ports of entry/exit).
e. Incentivizing research into the optimization of biohydrogen production from termite gut microbes, which would also contribute to reducing the impact of global warming and loss of biodiversity.

Pupil Participation

1. Class Discussion of the ecological and economic impact of termites

2. Pupil Stakeholder Awareness

a. Considering the positive impacts that termites have on the natural environment, is it wise to use pesticides for controlling the same species when they infest urban structures?
b. When taking into account the effects that livestock have on the environment through greenhouse gas emissions, what do you think might make termites a more sustainable option as "mini-livestock?"

3. Exercises

a. Humans have eaten insects for thousands of years, and many people still eat them, including termites, today. The Food and Agriculture Organization of the United Nations supports the use of insects as human food and livestock feed as a sustainable and healthy alternative to conventional protein sources. Would you eat termites? Why, or why not?
b. Termites use trophallaxis to share their gut microbes among colony members. What about their diet and lifestyle do you think makes it so important for them to participate in this behavior? Can you think of other animals that use trophallaxis or a similar behavior?

c. Which other animals do you know that need microbes in their guts to help digest their food?
d. Which other animals do you know that need microbes in their guts to obtain essential nutrients/growth factors, like vitamins?

The Evidence Base, Further Reading, and Teaching Aids

Enrico Bonatti 2011. Social insects: Bees, ants, and termites (Outreach practicum) https://cpb-us-e1.wpmucdn.com/blogs.cornell.edu/dist/7/3643/files/2013/09/Social-Insects-I-26beuxe.pdf
Strydhorst, N. 2015. Termite mounds: a grasslands climate change buffer. https://calvinchimes.org/2015/02/20/termite-mounds-a-grasslands-climate-change-buffer/
Banigan, M. 2017. At bug-eating festival, kids crunch down on the food of the future. https://www.npr.org/sections/thesalt/2017/09/14/550188017/at-bug-eating-festival-kids-crunch-down-on-the-food-of-the-future
Tolley, J, 2018. The Wisconsin energy-institute looks to termites for a biofuel breakthrough. https://btn.com/2018/03/13/the-wisconsin-energy-institute-looks-to-termites-for-a-biofuel-breakthrough-btn-livebig/
Wood, C. 2018. Termites built themselves a landfill the size of Great Britain. https://www.popsci.com/termites-brazil-landfill-mounds/Borunda, A. 2019. Cows and bogs release methane into the atmosphere, but it's by far mostly human activity that's driving up levels of this destructive greenhouse gas. https://www.nationalgeographic.com/environment/global-warming/methane/
Dasgupta, S. 2019. Termites help to protect tropical forests during drought, study finds. https://news.mongabay.com/2019/01/termites-help-to-protect-tropical-forests-during-drought-study-finds/

Glossary

Amino acids – The molecules from which proteins are synthesized in living organisms
Ammonia – NH_3; a molecular compound made up of nitrogen and hydrogen, which serves as a source of usable nitrogen for organisms, as opposed to atmospheric nitrogen (N_2). Ammonia is a product of the chemical reaction called "nitrogen fixation" which is performed by a number of microorganisms
Archaea – A domain of single-celled prokaryotic microorganisms. Archaea are well-known for their ability to thrive in inhospitable environments, like extremely hot hydrothermal vents in the ocean
Biofuel – Any fuel derived from living organisms and/or their waste (e.g., ethanol from corn)
Biodiversity – The variety of different living organisms in a particular ecosystem
Biopesticide – Pesticidal chemicals derived from living organisms
Bioreactor – A vessel (typically in reference to a man-made chamber) in which specific biological processes take place, usually to create biochemical products
Carbon cycle – The movement of carbon throughout the environment via respiration, emission, photosynthesis, and the decay of dead organisms

Climate change – Shifts in the temperature and weather patterns of the planet. Can occur naturally or be caused by human activity; most frequently discussed in the context of human activity that has negative consequences on the environment
Compost – The use of decayed organic matter as a natural fertilizer; generally in reference to an intentional process of recycling plant waste products
Ecosystem services – Benefits provided by nature to people
Eusociality – A strategy of social organization, most commonly seen in, but not entirely limited to, arthropods, in which a large group of related individuals called a "colony" participates in an advanced division of labor. Different groups of individuals within the society are divided into "castes," each of which provide different services to the group as a whole. In termites, there are: reproductive individuals, who produce young (queens, kings, and some "secondary" reproductive individuals); soldiers, who provide colony protection; and workers, who forage for colony resources and care for other castes
Fossil fuel – Fuels derived from the remains of ancient living organisms; e.g., coal and natural gases
Greenhouse gasses – Gases, e.g., carbon dioxide, which absorb and trap radiation in the form of heat from the sun in the Earth's atmosphere, causing "global warming"
Hybridization – The interbreeding of two closely related, but distinct, species or plant varieties
Invasive – Referring to an organism that has been introduced to a range it is not native to, particularly when its introduction negatively impacts beneficial native organisms in its introduced range, e.g., non-native plants or animals that out-compete or directly harm native species
Lignocellulose – A complex component of woody plant cell walls consisting of lignin and cellulose
Livestock – Any live animal that is raised to be used as a resource, e.g., farm animals, like cows, pigs, or chickens
Methane – A gas found in the Earth's atmosphere and the most prominent component of natural gas; it is emitted from livestock and human activity that results in the decay of organic matter. It is also considered a "greenhouse gas"
Methanotrophic – A feeding strategy in microorganisms that involves the breakdown of methane
Microbiome – All microorganisms associated with a particular habitat; most frequently, the term is used in reference to microbes associated with animal guts
Multigenerational – Referring to multiple generations, especially in the context of several generations of related organisms sharing the same living space
Nitrogen cycle – The movement of nitrogen through the environment in a variety of chemical forms, through biotic and abiotic systems
Nitrogen fixation – The microbial process of converting atmospheric nitrogen (N_2), which is unusable by most organisms, into organic compounds, such as ammonia (NH_3)
Non-renewable – Referring to resources that are not readily replaced or renewed; e.g., fossil fuels, which take millions of years to form naturally as opposed to resources such as solar power, which can be continuously harnessed without risk of resource depletion
Protist – Any eukaryote (organism with membrane-bound cell organelles) that is not an animal, plant, or fungus. They are generally microscopic and single-celled, but there are exceptions
Protozoa – Single-celled eukaryotes, sometimes referred to as "animal-like protists" as they are heterotrophic, meaning that they consume nutrients not synthesized through processes such as photosynthesis

Renewable – Referring to resources that are easily replaced/renewed, such as energy from living organisms, sunlight or wind. These resources are not expected to be as easily depleted as those that take a significant amount of time to form, such as fossil fuels that cannot be readily made
Soil aeration – The act of making soil accessible to the air, often through burrowing animals, like earthworms, termites, or mammals that dig holes in the ground, resulting in the movement of oxygen and/or carbon dioxide through soils from the atmosphere
Symbiont – Any organism living in symbiosis with another organism; see "symbiotic"
Symbiotic – Referring to the relationships between organisms of two or more different species. Symbiotic relationships can be positive, negative, or neutral. The main types of symbiotic relationships (also called symbioses) are: mutual, predaceous, parasitic, competitive, or commensal
Taxonomic group – Referring to any organizational level of the classification of living organisms; domains, kingdoms, phyla, classes, orders, families, genera, and species are all taxonomic groups at different organizational levels; could also be called "taxa"
Trophallaxis – The act of sharing digestive fluids between individual members of a subsocial or eusocial group of organisms. Trophallaxis is further defined as "stomodeal," if it is shared mouth-to-mouth, or "proctodeal," if gut fluids are exchanged from anus-to-mouth.