Tardigrades
(Some very tough little astronauts)

Can you fit an astronaut in a drop of water?
Only if it is a water bear!

Violeta Gallego-Rodríguez[1], Andrea Jurado-Muñoz[2] y Carmen Palomino-Cano[3]

[1]Uppsala University, Uppsala, Sweden, [2] Dairy Products Institute of Asturias (IPLA), Asturias, Spain, and [3]Tropical Health Institute of the University of Navarra, Navarra, Spain

Tardigrades

Storyline

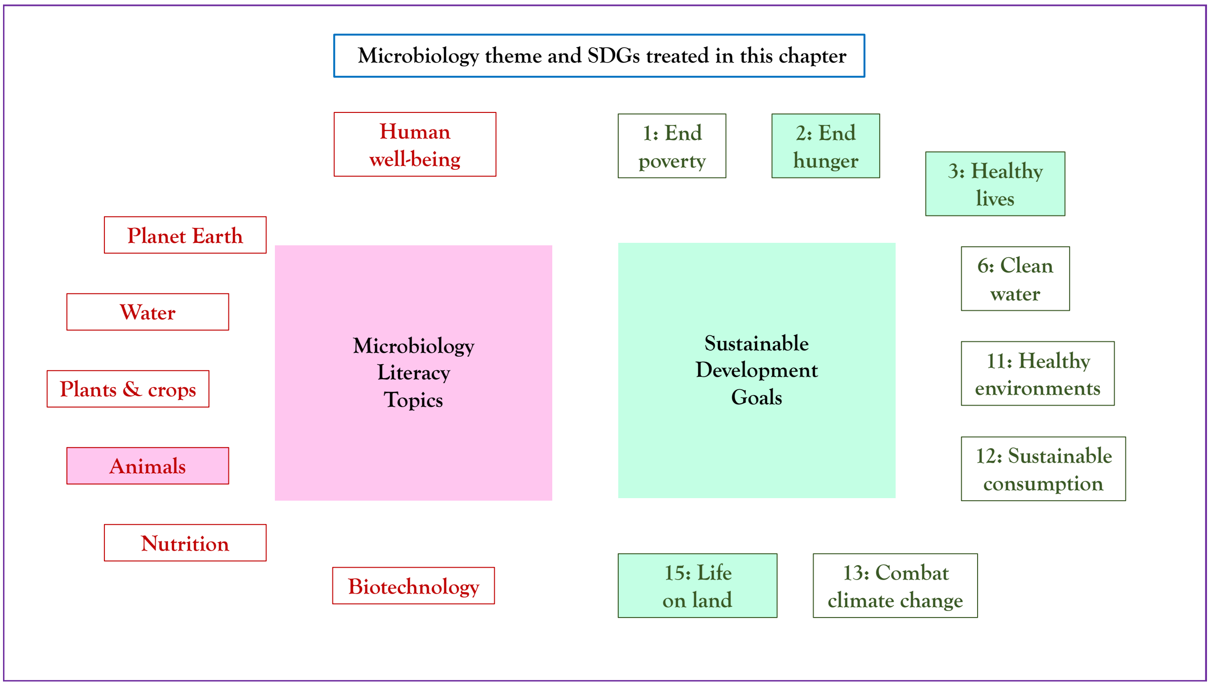
When we think of animals, the first ones that might come to mind are those we share our lives with – dogs, cats, fishes, cows, ants, birds, etc. – or learn about in school – lions, whales, sharks, tigers, etc. However, what about the ones that cannot be seen with the naked eye? There is a vast and diverse microscopic world surrounding us, and tardigrades are among the animals we might not think of at first. However, their extraordinary adaptations to the harshest environments leave no one indifferent.

Tardigrades, also referred to as water bears, are tiny transparent **invertebrates** that were discovered in the 18th century by the German scientist Johann August Ephraim Goeze. Their name Tardigrada comes from the latin word *tardigradus*, which means slow-moving, and refers to their strange and bear-like gait. These animals can survive in almost every type of environment we can think of, from deep oceans to the Himalayas, and even outer space.

In this topic framework, we are going to learn about the life cycle of these special animals, and try to understand the strategies that permit them to adapt to extreme environments, including outer space, and how their impressive features may be exploited to positively impact our society.

The Microbiology and Societal Context

The microbiology: role in food webs; contribution to the health of humans and other animals; plant and crops and biotechnology. *Sustainability issues*: end hunger; healthy lives; healthy environments; reduce pollution.



Tardigrades: the Microbiology

1. ***The water bear – the (almost) invisible bear.*** Microbes are by definition invisible to the naked eye – we need the help of a microscope that magnifies them so that they can be seen. But the immense diversity of life means that some organisms have sizes at the border of visibility of the human eye, which is about 0.1 mm. Tardigrade sizes vary from 0.05 to 0.5 mm (smaller than a grain of sand!) so, are just at the limit of visibility (if we know what we are looking for!). This issue of being neither one (visible) nor the other (invisible) is an important lesson in life for us to learn. For convenience, humans create categories – silos – that we can assign things to, like food we like and food we don't like. But we need to keep in mind that such categories are artificial – not natural – constructions which do not reflect the diversity of nature.

Tardigrades are small animals at the border of visibility. Should they be considered microbes? Or not? Well: microbiologists are very inclusive people and welcome everything that is small. Moreover, in order to see what a tardigrade looks like – how beautiful it is (see videos below) – we need a microscope, *so there you have it: tardigrades are microbes!*

There are many examples of microbes that can be seen under certain circumstances. For example, fungi are microbes and yet they produce fruiting bodies that everyone can see when they go into the woods in Autumn, into the supermarket to buy mushrooms for a risotto, or see black stains on the bathroom tiles. Green threads of microalgae in streams are another example. But tardigrades are special!

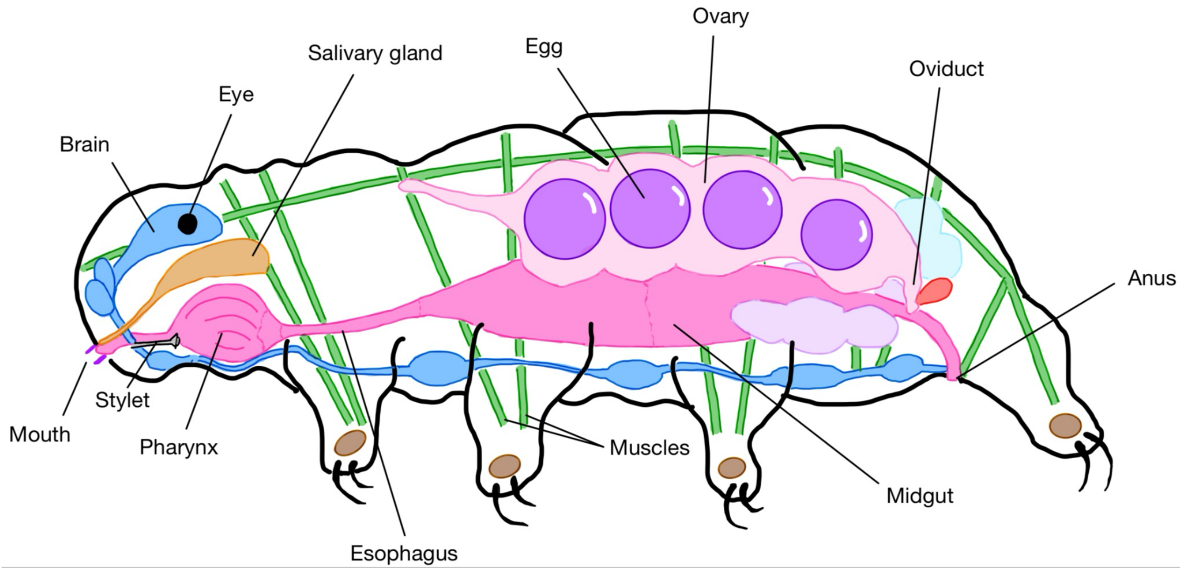
2. ***What do they look like?*** The body of tardigrades is divided into five segments and covered by a hard **cuticle**. As the animal grows, this cuticle must be shed, and its structure is a key feature used to classify these organisms. If the cuticle is smooth and lacks plates, the tardigrade is considered a member of the Eutardigrada group, while if the cuticle is armored with plates, the tardigrade is classified within the Heterotardigrada group.

Tardigrades move using muscles associated with their four pairs of legs, using their tiny claws to grip surfaces and prevent themselves from sliding. Inside their bodies, tardigrades have a cavity known as the **hemocoel**, which is filled with a colorless fluid called **hemolymph**.

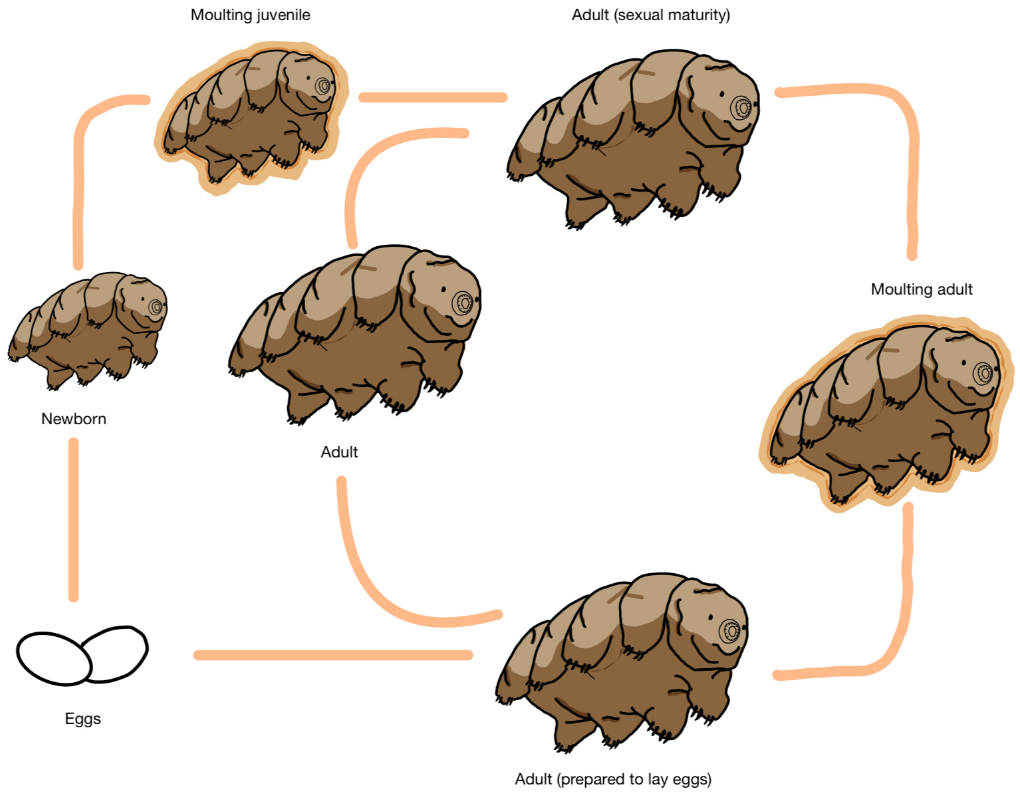
Like other animals, tardigrades possess respiratory and circulatory systems, but their small size comes with very interesting features. They do not have specialized respiratory organs (like lungs or gills); instead, they exchange gases across the **epidermis** and cuticle. They also lack a heart or other circulatory organs - instead, circulation is carried out by the movement of the hemolymph and the cells within the hemocoel.

However, there is a very important organ that tardigrades do possess: a brain. Adult tardigrade brains can contain between 200 and 370 neurons - similar to the brain of some adult wasps - and it only occupies approximately 1% of the body volume. Their brain is considered simpler compared to that of insects of similar size, because other structures linked to brain activity, such as eyes and their associated nerves, appear to have very simple morphologies in tardigrades.

Regarding their digestive system, tardigrade's biggest organ is typically the gut. It is divided into a foregut (which includes the buccopharyngeal apparatus and esophagus), a large midgut, and a smaller hindgut. Depending on the species and their diets, these structures allow them to feed on plant cells, yeast, algae, bacteria, nematodes, etc.



3. ***How do they reproduce: the tardigrade life cycle?*** Tardigrade reproduction relies on fertilized or unfertilized eggs, and both **amphimixis** (sexual reproduction) and **parthenogenesis** (asexual reproduction) have been described in this group. Females possess a single ovary that varies in size depending on age and reproductive stage, while males have testes whose shapes differ between heterotardigrades and eutardigrades. Some species are hermaphroditic, possessing a single **ovotestis** that usually contains both male and female **germ cells**, though in some cases or life stages one type can predominate over the other one.



The different stages of the tardigrade life cycle. Drawing based on Altiero et al.

One well-studied example of a tardigrade life cycle is that of female eutardigrades, which consists of several stages. Once the embryo is fully developed and hatches from the egg, the juvenile tardigrade undergoes successive moults (typically two or three). After each moult, its body length increases until it reaches its maximum size and, eventually, sexual maturity. At this point, the female produces and lays eggs and continues to undergo adult moulting throughout her life.

Information about mating and fertilization is limited. In some species, the male uses his sensory organs to stimulate the female to lay eggs, which are then fertilized externally. In others, fertilization occurs before egg **oviposition**. In hermaphroditic tardigrades, both self-fertilization and cross-fertilization have been observed.

4. ***Where tardigrades live and what they eat.*** Tardigrades are incredibly versatile animals, capable of surviving in an astonishing variety of environments -terrestrial, freshwater, and marine- as long as there is enough water for activity or stable conditions for survival in a dormant state. We will learn more about this last aspect soon!

On land, these microscopic creatures are commonly found in mosses, lichens, liverworts, and leaf litter. Such microhabitats provide ideal conditions not only for breathing but also for finding food. Tardigrades feed using their pharyngeal bulb, piercing prey with tiny stylets and sucking out cellular contents. Their diet varies widely depending on the species; some consume algae, moss cells, plants, protozoa, bacteria, and organic detritus, while predatory species feed on small metazoans such as nematodes, rotifers, and even other tardigrades. Even as they hunt, tardigrades themselves can become prey for **collembolans**, nematodes, mites, spiders, and insect larvae.

Tardigrades are not limited to mosses and leaf litter; they also inhabit moist soils and litter layers, often several centimeters deep, especially places that retain water and nutrients. They occupy tiny spaces between soil particles, under decaying wood, or within humus layers, where stable microclimates help them survive droughts. In extreme terrestrial environments, they have been recorded on high-altitude mosses in mountain ranges such as the Himalayas, as well as in deserts where dew or fog provides intermittent moisture.

Even human-dominated environments can host tardigrades, albeit at lower densities. Urban niches such as wall crevices, rooftop mosses, gardens, sidewalks, and accumulated debris offer the intermittent moisture these creatures need. These observations highlight their ability to exploit anthropogenic ecosystems and persist in habitats shaped by human activity.

In aquatic habitats, tardigrades are equally versatile. Some species thrive in freshwater lakes, streams and ponds, while others inhabit marine environments. They may cling to submerged vegetation, dwell within sediments or swim freely in the water column.

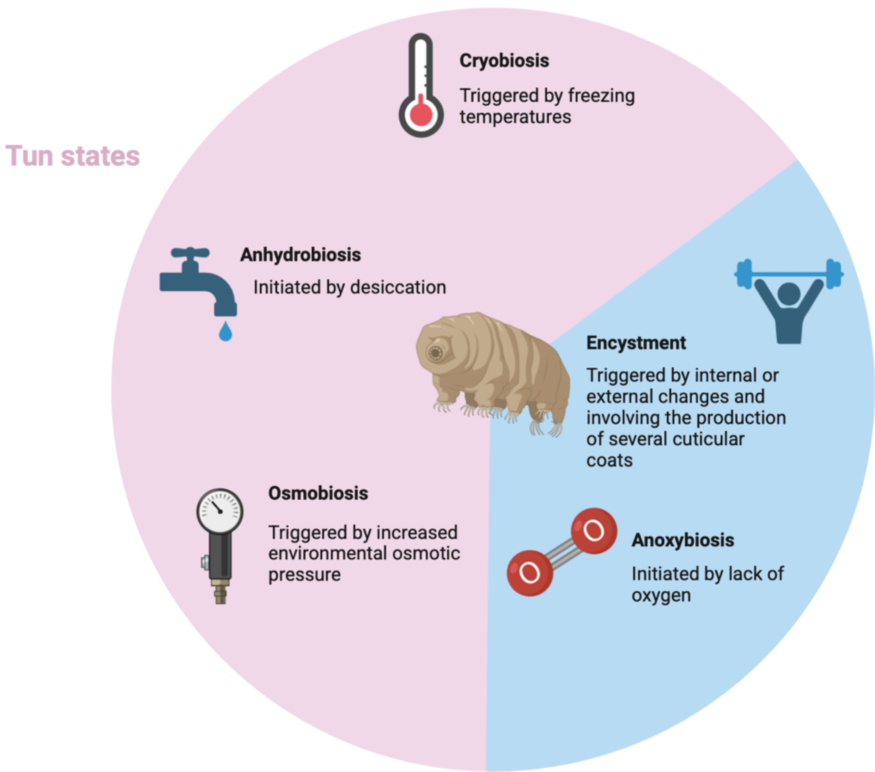
5. ***Life in extreme environments.*** Tardigrades are known for being either extremophiles or extremotolerant. Extremophiles are organisms that thrive in and require very harsh conditions that would be detrimental for most life forms on Earth, while extremotolerants are the ones with the ability to survive extreme environments but require milder conditions to grow. Tardigrades are considered polyextremophiles or polyextremotolerants because they are able to survive different types of extreme conditions, such as high X-ray radiation, high pressure, vacuum, and very high and low temperatures.

The main strategy that allows their survival in such conditions is entering a reversible state of arrested metabolism called **cryptobiosis**. Species of tardigrades capable of surviving extreme environments enter this **ametabolic** state in response to stress factors. There are several cryptobiotic sub-states, depending on the environmental cues that signal the tardigrade to slow down its metabolism:

a. anhydrobiosis: initiated by desiccation
b. osmobiosis: initiated by increased environmental osmotic pressure
c. cryobiosis: initiated by freezing
d. anoxybiosis: initiated by lack of oxygen
e. chemobiosis: initiated by presence of toxic agents in the environment.

However, more evidence is required to confirm that anoxybiosis and chemobiosis are true forms of cryptobiosis. In any case, anhydrobiosis, osmobiosis and chemobiosis are states in which tardigrades have been observed to enter in a **tun state** in response to environmental stress. It is thought that, by doing this, extremotolerant species **constitutively** express **bioprotectants** required for survival in the cryptobiotic state. **Diapausing** eggs have also been reported as a strategy to survive environmental deterioration, hatching only after a sequence of stimuli (for instance, dehydration followed by rehydration).

Tardigrades not only have strategies to survive exogenous stimuli, but also to endogenous (internal) ones. This is achieved by a process known as encystment, a form of dormancy triggered by internal or external changes and involving the production of several cuticular coats along with morphological changes. Nevertheless, some species do not need to arrest their metabolism to tolerate extreme conditions. Certain tardigrades can withstand drastic changes in osmolarity, freezing temperatures, and extreme levels of radiation - although high temperatures seem to greatly affect the survival of these animals, probably by destabilizing key biological macromolecules.



The different survival strategies that can be found in tardigrades. Created in Biorender.

6. ***Survival in outer space.*** Tardigrades have been known for their ability to withstand tough conditions for a long time. This ability drove Swedish and German scientists to come up with the experiment "Tardigrades in space" (TARDIS). TARDIS had the goal of studying if these animals were able to survive the space environment. To do so, in September 2007, 3000 tardigrades were sent into space on ESA's orbital Foton-M3 mission. Water bears proved to be capable of surviving space vacuum (which entails extremely high dehydration and cosmic radiation), raising many questions related to how marine and terrestrial animals are prepared for exposure to space conditions, and which mechanisms are behind this ability. This information could be very valuable in space research, for instance, by allowing us to come up with new ways of protecting food and medicines in outer space and thus opening the door for long duration missions.

7. ***A positive impact in society.*** Apart from their potential applications in space research, studying tardigrades' extraordinary features could help address some of today's major challenges. One of the characteristics of these organisms that has drawn the most attention is their ability to survive desiccation, as the lack of water is typically one of the most detrimental conditions for life (the bodies and cells of most organisms, including us, consist of 60-95% water). Understanding the molecular mechanisms behind their survival strategies is promising for developing new preservatives that could improve the storage of vaccines. In fact, certain proteins found in tardigrades have been shown to protect the **enzymatic** component of some drugs from damage caused by desiccation or freezing.

Moreover, these proteins not only hold importance in the biomedical field, but some researchers are also applying them in other organisms, such as plants, to help create crops more resilient to drought, or certain diseases, turning tardigrades into what is known as **biofertilizers**. Biofertilizers are a great alternative to chemical fertilizers, since they use living soil microbes that enhance plants' growth and are less likely to have a negative effect in ecosystems, such as pollution and reduction of biodiversity. The main problem of biofertilisers is that the microorganisms used normally die of desiccation when they are packed. Research in tardigrades has been of great use in creating new materials that prevent this from happening.

Relevance for Sustainable Development Goals and Grand Challenges

Tardigrades are relevant to several SDGs, including:

- **Goal 2. End hunger.** Understanding how tardigrades survive desiccation could help promote more sustainable agriculture and contribute to food security. A specific family of tardigrade proteins, known as secretory-abundant heat soluble (SAHS) proteins, has been shown to have potential in protecting plant growth-promoting bacteria, such as *Rhizobium tropici*, against dessication. This opens the door to developing more durable microbial fertilizers.

- **Goal 3. Healthy lives.** Some tardigrade proteins have biomedical relevance. Apart from using proteins that protect against desiccation to improve vaccine storage, other proteins that protect DNA from radiation damage (known as Dsup) are promising in biomedical fields such as cancer research. The great majority of cancer treatments involve radiation therapy at some stage, which tends to harm both cancerous and healthy cells. A study performed with these tardigrade proteins, which were delivered to mice before radiation exposure, showed that the DNA of the mice treated with Dsup was much better protected from breakage than that of untreated mice

- **Goal 15. Conserving life on land.** Chemical fertilizers are commonly used to provide essential nutrients to plants to promote their growth in agriculture. However, their misuse has several adverse effects, including soil **acidification**, soil degradation, decreased microbial diversity, and an increase in the amount of harmful chemicals in the soil. Replacing these types of fertilizers with microbial alternatives can improve the microbial richness and diversity, enhance soil fertility, and increase the resilience of that ecosystem.

The Evidence Base, Further Reading and Teaching Aids

Tardigrade videos

- https://www.youtube.com/watch?v=IH3ABle9k7A
- https://www.youtube.com/watch?v=kux1j1ccsgg
- https://www.youtube.com/watch?v=IxndOd3kmSs&t=49s
- https://www.youtube.com/watch?v=dork_85Q8uI&t=116s

Reviews for the general public

- https://projects.research-and-innovation.ec.europa.eu/en/horizon-magazine/dried-out-tardigrades-could-point-way-drug-preservation-resilient-crops
- https://www.americanscientist.org/article/tardigrades
- https://www.esa.int/Science_Exploration/Human_and_Robotic_Exploration/Research/Tiny_animals_survive_exposure_to_space
- https://www.nasa.gov/humans-in-space/microscopic-superheroes-to-help-protect-astronaut-health-in-space/
- https://www.nature.com/articles/d41586-025-01971-7

Scientific articles for deeper study

Altiero, T., Suzuki, A. C., & Rebecchi, L. (2019). Reproduction, development and life cycles. In *Water bears: the biology of tardigrades* (pp. 211-247). Cham: Springer International Publishing.

Gross, V., Treffkorn, S., Reichelt, J., Epple, L., Lüter, C., & Mayer, G. (2019). Miniaturization of tardigrades (water bears): morphological and genomic perspectives. *Arthropod structure & development*, 48, 12-19.

Guidetti, R., Altiero, T., & Rebecchi, L. (2011). On dormancy strategies in tardigrades. *Journal of Insect Physiology*, 57(5), 567-576.

Jönsson, K. I., Holm, I., & Tassidis, H. (2019). Cell biology of the tardigrades: current knowledge and perspectives. *Evo-Devo: Non-model Species in Cell and Developmental Biology*, 231-249.

Lim, S., Reilly, C. B., Barghouti, Z., Marelli, B., Way, J. C., & Silver, P. A. (2024). Tardigrade secretory proteins protect biological structures from desiccation. *Communications biology*, 7(1), 633.

Møbjerg, N., Halberg, K. A., Jørgensen, A., Persson, D., Bjørn, M., Ramløv, H., & Kristensen, R. M. (2011). Survival in extreme environments–on the current knowledge of adaptations in tardigrades. *Acta physiologica*, *202*(3), 409-420.

Weronika, E., & Łukasz, K. (2017). Tardigrades in space research-past and future. *Origins of Life and Evolution of Biospheres*, *47*(4), 545-553.

Glossary

Acidification: is the process in which a system (such as soil or water) becomes more acidic as its pH declines. In agricultural soils, this often results from the excessive use of chemical fertilizers that generate acidic compounds during their breakdown, contributing to soil degradation and a reduction in microbial diversity.
Ametabolic: refers to a condition in which an organism's metabolic activity is essentially halted or becomes undetectable, typically as a strategy to withstand extreme environmental stress.
Amphimixis: reproduction where two different individuals each provide a gamete (an egg and a sperm), and these two gametes fuse to form a new organism
Biofertilizers: Natural substances containing living microorganisms that promote plant growth by increasing the availability of nutrients in the soil. They are an eco-friendly alternative to chemical fertilizers.
Bioprotectants: Substances, often derived from living organisms, that help protect plants or animals from stress, diseases, or harmful environmental factors. They enhance resilience without relying on synthetic chemicals
Cryptobiosis: A reversible physiological state in which an organism's metabolic activities nearly stop, allowing it to survive extreme environmental conditions such as dehydration, lack of oxygen, or extreme temperatures. *Unlike *diapausing*, cryptobiosis is an emergency response to extreme stress and not part of the normal life cycle.
Constitutively: Describes a process or characteristic that occurs continuously or is always active, regardless of external conditions. For example, a constitutively expressed gene is always active, producing its protein continuously, regardless of environmental signals.
Cuticle: A non-cellular protective outer layer, mainly composed of proteins and chitin in many invertebrates, that covers the body, provides structural support, and helps prevent water loss and damage from the environment
Diapausing: A physiologically programmed state of suspended development or reduced metabolic activity that allows an organism or its eggs to survive unfavorable environmental conditions. *Unlike *cryptobiosis*, it is part of the normal life cycle and not just a response to extreme stress.
Enzymes: Biological molecules, usually proteins, that act as catalysts to speed up chemical reactions in living organisms without being consumed in the process.
Epidermis: The outermost cellular layer of an organism, covering the body or organs, which provides protection and can be involved in secretion, absorption, or sensory functions. In tardigrades, the epidermis lies beneath the cuticle.

Germ cells: Reproductive cells of an organism, such as sperm or eggs, that carry genetic information to the next generation.
Hemocoel: A body cavity typical of many invertebrates with an open circulatory system; it contains hemolymph instead of blood circulating through closed vessels.

Hemolymph: The circulatory fluid in invertebrates with an open circulatory system; it transports nutrients, hormones, and waste, and plays a role in immune defense.
Invertebrates: Animals that lack a backbone and internal bony skeleton; they include arthropods, mollusks, annelids, nematodes, tardigrades, and others.
Oviposition: The process of laying or depositing eggs by an oviparous organism.
Ovotestis: A hermaphroditic gonad that contains both ovarian and testicular tissue, capable of producing eggs and sperm simultaneously.
Parthenogenesis: A form of asexual reproduction in which offspring develop from an unfertilized egg, without the need for fertilization by a male. For example, some species of insects, reptiles, and even certain crustaceans and tardigrades can reproduce this way.
Tun state: State in which tardigrades retract their limbs and decrease water storage to increase chances of survival.