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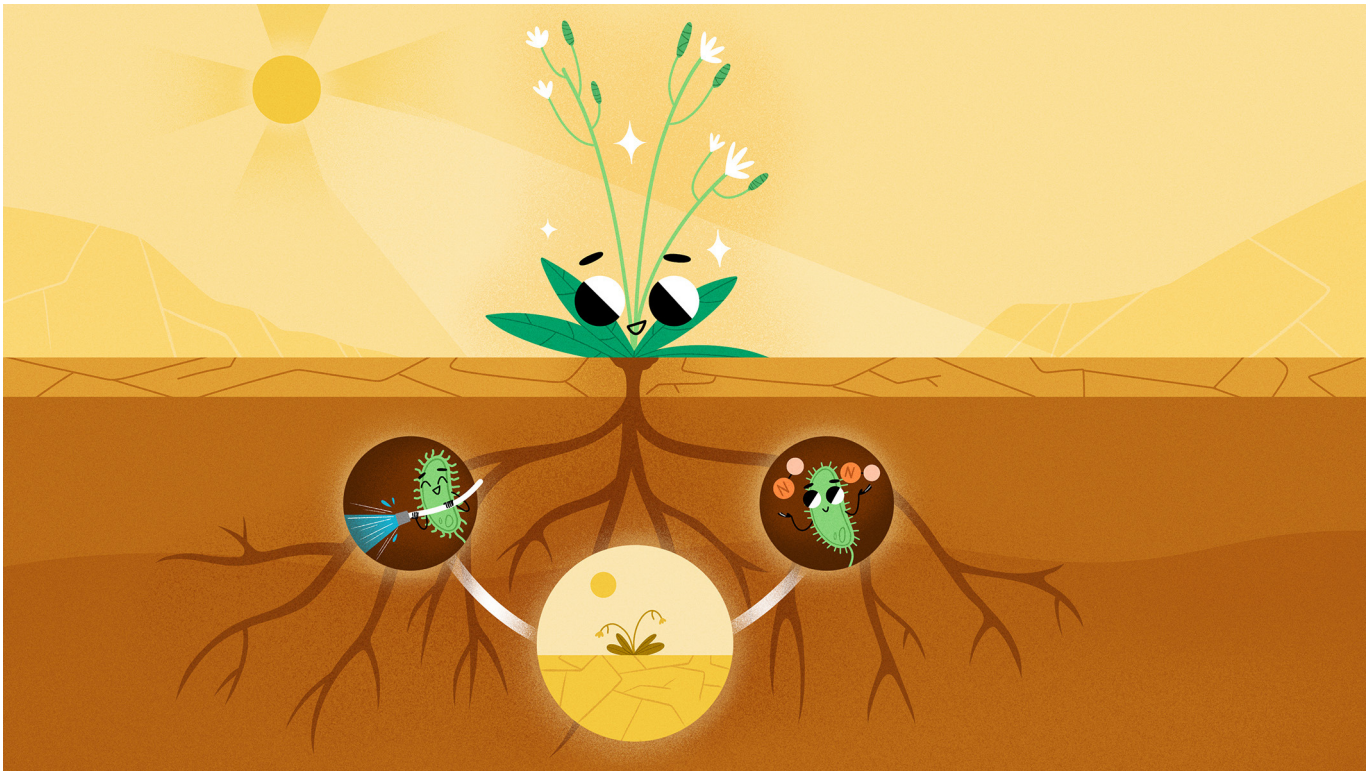

HOW PAST STRESS HELPS MICROBES BENEFIT PLANTS

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People are exposing nature to stress, including pollution and drought. Many plants can survive these stressors because they live with helpful microbes that form communities on and inside plants. How well-microbial communities can help stressed plants depends on whether the microbes have experienced the stress before—which is called their *stress legacies*. For example, past drought (lack of rain) can favor drought-resistant microbes, which leads to more drought-resistant microbial communities. In turn, these microbial communities can better help plants under future drought stress. Thus, microbes that experienced particular stresses in the past can better help plants survive stress in the future. This means stress legacies of microbial communities matter for the health of our environment.

A CHANGING PLANET

Think of all the ways humans impact the environment: warming the air, polluting the soil, and increasing saltiness in the water. These stresses are challenging because some plants and animals cannot adapt quickly enough to survive. Losing key species can be devastating for the health and functioning of Earth's **ecosystems**.

ECOSYSTEM

All organisms living together in a certain time and place and interacting with their surrounding environment.

MICROBES: HIDDEN PLAYERS IN ECOSYSTEMS

Our world is made up of much more than just plants and animals. Microbes, like bacteria, fungi, and even viruses, are invisible to the naked eye. But they are super diverse! Researchers estimate that there are over 10,000,000,000,000,000,000,000,000,000 bacteria in the ocean. That is more than 100 million times the number of stars in the known universe [1]! Even though microbes are small, they are crucial to the benefits ecosystems provide.

Many microbes live closely with plants and animals, forming **symbiotic** relationships. For every living thing you can see, there are countless microbes living in, on, or near it—which is true even for humans! Did you know that we have about as many bacteria living in and on our bodies as we have our own human cells [2]?

SYMBIOTIC

Refers to two or more species living closely together. That relationship is called a symbiosis.

Microbes help us in return for the resources and services we provide them. These types of mutually beneficial relationships are called **mutualistic**. In fact, many organisms need microbes to live. For example, an orchid plant cannot survive without tiny fungi living in symbiosis with its roots. These microbes help orchids access crucial nutrients in exchange for sugars that orchids can produce [3]. In other cases, animals and plants do not require mutualistic microbes to survive in *favorable* conditions, but they cannot tolerate *stressful* conditions without the help of microbes. For example, the grass called Chinook brome can only live in dry habitats with the help of the tiny fungi living in its leaves (a type of **endophyte**), even though the grass can survive without these fungi in wetter habitats (Figure 1) [4]. In a world where humans are constantly introducing stressors into ecosystems, microbes are an important part of how plants and animals respond to stress. Imagine how many plants and animals would not be here without microbes!

MUTUALISTIC

Describes an interaction between species that is beneficial for all partners.

ENDOPHYTE

A microbe that lives inside a plant without causing disease. There are many types of endophytes, including both fungi and bacteria. Different endophytes live in different parts of plants.

MICROBES AS PLANT HELPERS

We rely on plants for food, wood, paper, and many other things. In fact, they even produce the oxygen that we breathe! But plants are rooted in the ground and cannot move from place to place. This means if their environment changes, they cannot escape. Therefore, they must find some way to adapt where they are. Imagine being outside on a hot

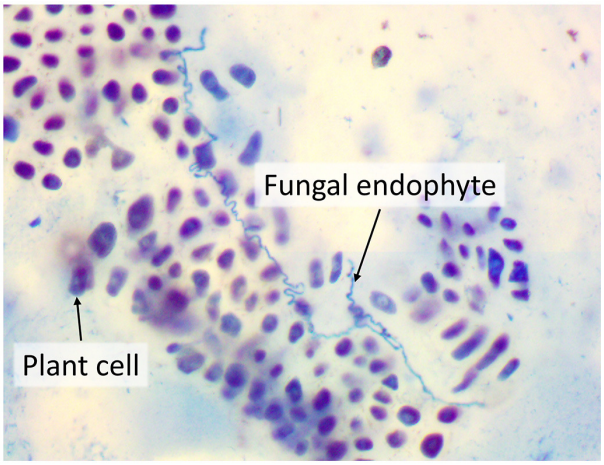

Figure 1

A dissected Chinook brome seed and its fungal endophyte, enlarged 200× with a microscope. Fungal endophytes are fungi that are small enough to live inside a plant, but do not cause disease. The type of fungal endophyte in this picture lives in the leaves, stems, and seeds of plants and can help those plants survive in dry environments (photograph taken by Vicki Li).

day—you might try to escape the heat by finding shade or by heading indoors. A plant cannot do that.

This is where stress-relieving microbes come into the picture. **Microbial communities** are groups of microbes living together in a certain time and place. Different microbial communities can contain different species of bacteria, fungi, and viruses. They can also differ in the functions they perform. For example, some microbial communities might have a lot of microbes that help plants get nutrients, and other microbial communities might have a lot of microbes that break down the remains of dead organisms.

MICROBIAL COMMUNITY

Groups of microbes living together in the same place and at the same time. Different microbial communities can have different types of microbes present or perform different kinds of functions.

Microbial communities play a big role in how plants behave. For example, some contain microbes that help plants reach water in the soil, while others have microbes that make plants taste bad to insects (Figure 2). Plants living with these microbial communities might be able to survive drought or insect outbreaks more easily. Since there are so many microbes with so many beneficial abilities and some can move around, they provide an alternative way for plants to respond to stress. This makes microbes really important for helping plants survive in stressful environments!

STRESS LEGACIES OF MICROBIAL COMMUNITIES AND WHY THEY MATTER

A **stress legacy** describes what stresses organisms have experienced before, which can affect how they might respond to stress later. Organisms that have experienced a stressor before are more likely to be used to it, making them more resistant in the future.

STRESS LEGACY

When organisms have experienced stresses in the past, which can affect how they behave when stressed later.

Now let us think about microbes and plants. The stresses that microbial communities have experienced before (their stress legacy) can affect

Figure 2

Plants live in symbiosis with microbial communities that can perform various beneficial functions. Nitrogen-fixing bacteria capture nitrogen in the air so plants can use it for nutrition. In return, they receive plant-made sugars. Mycorrhizal fungi also receive sugars, and they help plants capture phosphorus and water from the soil. Endophytes living inside leaves or roots rely on plants for sugar and for reproduction. Some of these endophytes (like the one in Figure 1) help plants survive in dry environments. Other microbes live in plant nectar. All these microbial communities can affect plant health (figure created with BioRender).

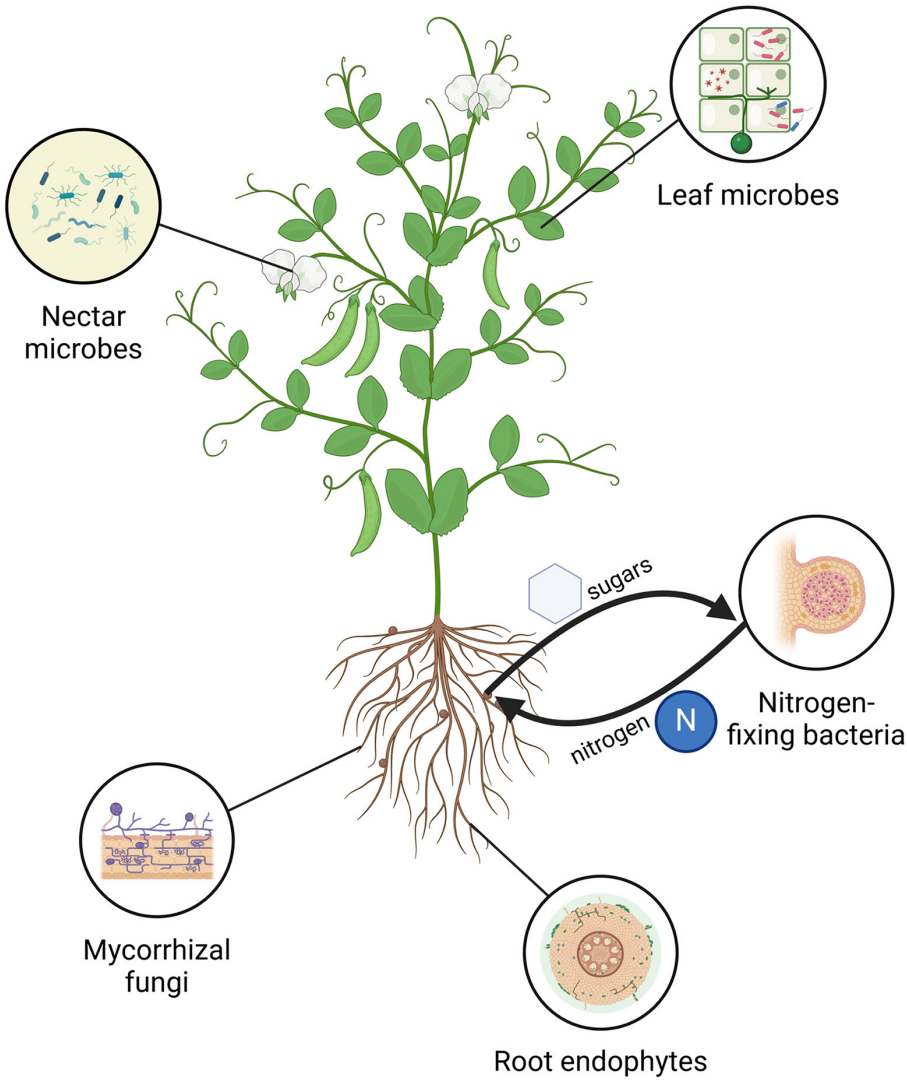

Figure 2

how well they can help plants under that stress in the future. For example, trees in a dry place are more likely to survive when planted with soil microbes from a dry place. Trees in a cold place are more likely to survive when planted with microbes from a cold place [5]. Similarly, mangroves—trees that protect coastlines and provide habitat—grow better in stressful saltwater when the fungi in their leaves are from saltier places [6]. This shows that the stresses microbes have experienced before really do matter for helping plants survive and thrive in stressful conditions!

SELECTION

Greater survival and reproduction of individuals with traits that are beneficial in a particular environment. These traits must be able to be passed down from parents to offspring.

HOW STRESS LEGACIES SHAPE MICROBIAL COMMUNITIES

How do stress legacies work? Past stressors can change microbial communities in ways that make them function better under stress, which is called **selection**. This can happen at two levels: by changing

what microbes are there (at the community level) and by changing what the microbes can do (at the genetic level) [7].

Past stress can select for which microbes are present in a community. Imagine your friends for a moment. You might have one friend group that gets together often to play basketball, and another group that you play video games with. Similar to how certain groups of people are good at certain things, certain groups of microbes are good at certain things, too. Past stress can select which microbes are present at the community level by favoring groups of microbes that help plants grow better under stress (Figure 3).

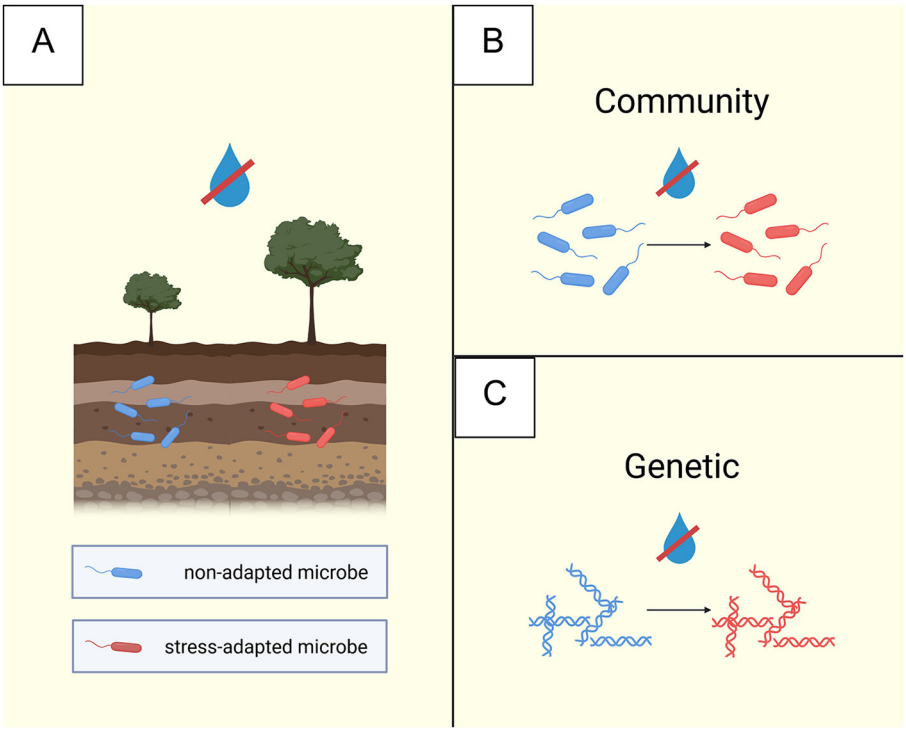

Figure 3

Figure 3

Stress legacies can change microbial communities so they function better and provide more benefits to plants under future stress. **(A)** Microbial communities that have experienced stress in the past, and thus have a stress legacy, can help plants better under future stress. For instance, microbes with past drought experience can increase tree survival under new drought. Stress legacies provide these benefits under future stress by changing microbial communities through selection on: **(B)** which microbes are present and **(C)** which genes are present. Red microbes and genes represent those that have been selected for by past drought (figure created with BioRender).

Stress legacies also act at a genetic level to change **genes**, which determine what microbes can do. Using your friends as an example again, imagine if being taller makes you a better basketball player and being good at puzzle-solving makes you better at video games. Then your friend group that plays basketball together would probably have a lot of tall people, and your friend group that plays video games would probably have a lot of people who enjoy solving puzzles. In this example, groups of people are good at certain things because of what each person is capable of.

Similarly, microbial communities are good at certain things when they have microbes that are capable of certain functions. If microbes have genes that make them stress resistant, stress legacies can select for those microbes and make them more common in microbial

GENES

Sections of DNA that provide instructions for building proteins. Ultimately, genes help determine the traits of an organism.

communities. That means even more microbes in the community become resistant to stress. By changing microbial communities at the genetic level, stress legacies make them more resistant to stress so they can better provide benefits to plants when future stressors occur (Figure 3).

MICROBES, PLANTS, AND A CHANGING WORLD

Humans are introducing new and stronger stressors into ecosystems. This can harm plants, which are crucial to life on Earth. Helpful microbes play a big role in allowing plants to tolerate stress.

Because stress legacies can change microbial communities, when studying and predicting how plants might respond to stress, we must also think about microbes and their stress legacies. Plants might not need just *any* microbes to survive stressors. They may specifically need microbes that have survived those same stressors before. And when plants survive stress, that helps the birds and squirrels and other animals that need the plants, too. Ultimately, the stress legacies of microbial communities are key to ecosystem health in a changing world.

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YOUNG REVIEWERS

MAYTE, AGE: 10
I like cooking, playing with bugs in the garden and my favorite subject is math. I also like shopping and hanging out with my friends.

JOCELYN, AGE: 15
I like animals and plants and go out to discover new traditions and cultures. My favorite subjects at school are chemistry and mathematics.

PEACE ACADEMY, AGES: 9–10
We are a friendly, nice, and smart class. We love to have fun and are trustworthy. We love when we do fun projects where we can explore and learn new things.

AUTHORS

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Vicki is a Ph.D. student at the University of Miami who studies microbial function and interactions with plants under environmental stress, with the goal of understanding plant responses to global change and the role that microbes play in ecosystems. This includes trying to understand how stress legacies work and how they can improve plant health in a changing world, which can involve months- or even year-long experiments stressing microbiomes. Vicki also enjoys music, reading, and carbonated beverages. *li07vicki@gmail.com

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Michelle is an associate professor at the University of Miami. She studies the ecology and evolution of interactions among plants and microbes at scales ranging from genes to ecosystems. The goal of her research is to understand the role of these species interactions in maintaining a functioning environment, restoring and protecting imperiled habitats, and predicting responses to environmental change. Michelle started studying how stress legacies affect plant-microbial interactions as a way to predict when microbes will be able to help plants faced with changing environments. She has conducted research on legacy effects of stressors like fire and high salt using a combination of field surveys, 50 years of environmental data, and field and greenhouse experiments with microbes and native plants like mangrove trees. When she is not busy with research and teaching, she enjoys traveling, hiking, volunteering at the local children's garden club, listening to audiobooks of epic fantasy novels, and spending time with her family.