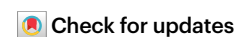


# Climate extremes disrupt fungal–bacterial interactions

Jingjing Shi & Madhav P. Thakur



Climate changes can destabilize soil microbial communities, but compound and sequential extreme climate events will magnify the destabilizing effects to other trophic levels – thereby impacting terrestrial biodiversity and ecosystem functioning.

Soil microbiomes, which are mainly composed of fungi and bacteria, maintain vital ecosystem functions, ranging from food production to climate change mitigation. Fungi and bacteria share a close spatial neighbourhood in the soil, and depend on each other for survival and fitness. However, they also engage in negative interactions<sup>1</sup>. Broadly, fungi and bacteria in the soil interact and impact ecosystem functioning in three ways: physical interactions, metabolic interactions and eco-evolutionary interactions (Fig. 1). These interdependent fungal–bacterial interactions (FBIs) feedback to one another, and the strength and impact of these interactions vary with changing abiotic conditions.

One of the major forms of physical interactions occurs through the attachment of bacteria to fungal hyphae and bacterial dispersal along hyphae<sup>2</sup>. The fungal hyphal network has been shown to increase the spatial intermixing of different bacterial strains, and, therefore, is important for regulating bacterial diversity<sup>3</sup>. Metabolic interactions between fungi and bacteria involve cross-feeding; in this case, bacteria utilize hyphal exudates as carbon (C) resources for growth, while fungal hyphae can absorb essential nutrients such as phosphorus (P) and nitrogen (N) released during P and N mobilization by bacteria<sup>4</sup>. Physical and metabolic interactions between fungi and bacteria often determine their eco-evolutionary interactions. Fungal hyphae-mediated bacterial dispersal can promote horizontal gene transfer (HGT) among bacterial cells<sup>3</sup>, and thereby drive rapid evolution in bacteria<sup>5</sup>. For example, HGT between arbuscular mycorrhizal fungus (*Diversispora epigaea*) and its endosymbiotic bacteria, known as Mollicutes or *Mycoplasma*-related endobacteria, have recently been found through comparative genome analysis. More specifically, *D. epigaea* acquired genes that could function in defence against foreign DNA or viruses from endobacteria; and the endobacteria acquired several genes that could be involved in fungal metabolism, such as those encoding chitin deacetylase, glycosyltransferase family proteins, chitin synthase and malic enzyme<sup>6</sup>. Physical interactions between fungi and bacteria can also affect their metabolic interactions. For instance, the attachment of *Bacillus subtilis* on the hyphae of *Aspergillus niger* resulted in a decrease in the antifungal and antibacterial metabolism of *B. subtilis* and *A. niger* at the transcriptional level, respectively<sup>7</sup>. Taken together, such feedback among the three types of FBI is central to understanding the structure and functioning of soil microbiomes.

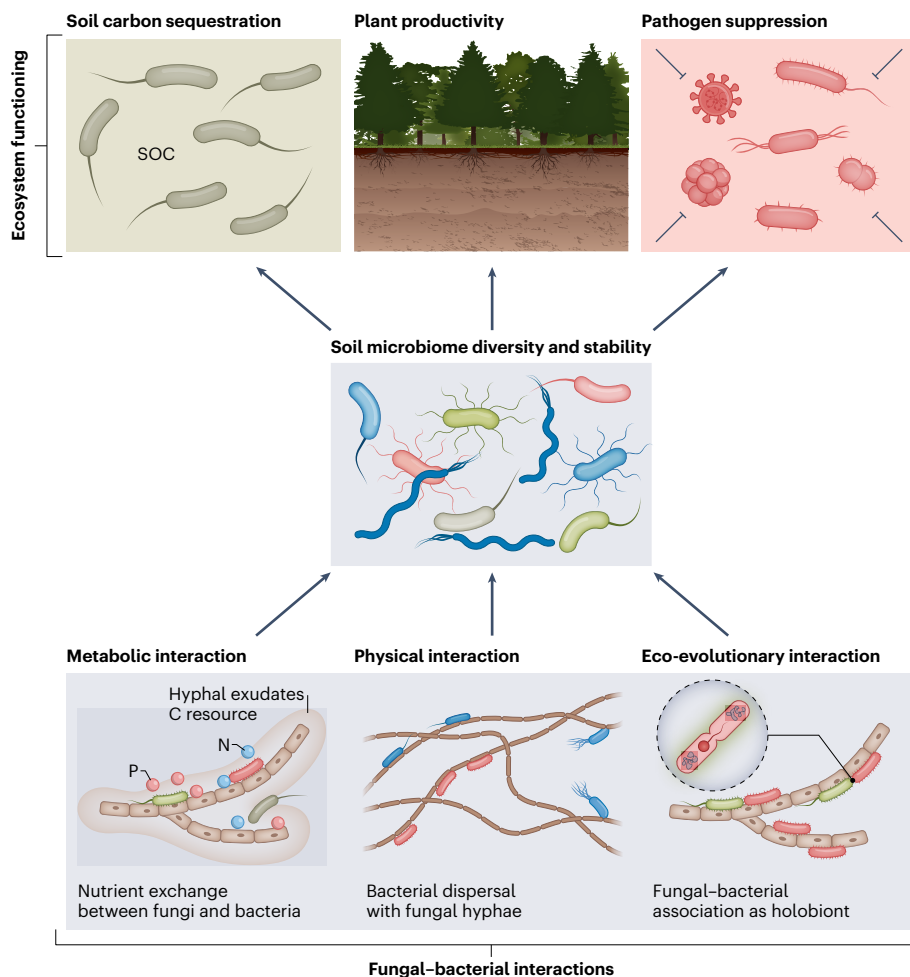
## Effects of climate extremes on soil fungi and bacteria

Recent increases in the frequency and magnitude of climate extremes, such as heatwaves and prolonged periods of drought, dramatically alter the structure of soil microbial communities. Studies have shown soil bacteria and fungi to exhibit differential responses to a given climate extreme. For instance, soil bacterial communities responded more strongly to extreme droughts than fungal communities, with a relative increase of Actinobacteria and a decrease of Acidobacteria<sup>8</sup>. A global-scale study across 80 drylands also noted that aridity lowers soil bacterial diversity by reducing groups such as Acidobacteria and Verrucomicrobia, mainly due to low soil organic carbon in dry soils<sup>9</sup>. A recent heatwave and drought in Central Europe strongly impacted the community structure, assembly and function of soil microbiomes in croplands and grasslands by increasing groups such as Actinobacteria, Eurotiales (fungi) and Vilmaviridae (viruses)<sup>10</sup>. Interestingly, the same study also reported that the soil microbiome recovery after these climate extremes was faster in grassland soils than in cropland soils, highlighting the habitat-dependent microbiome stability against climate extremes<sup>10</sup>. Indeed, compound and sequential climate extremes could constrain the recovery of soil microbiomes to pre-extreme event levels.

A major research gap so far is quantifying various FBIs under the influence of climate extremes and subsequently linking them to soil microbiome stability. Previous studies on bacterial and fungal network responses to climate extremes provide a broad picture of how FBIs might be shifting under the influence of climate extremes. For instance, bacterial co-occurrence networks are more disrupted by drought than fungal networks<sup>11</sup>, indicating a stronger breakdown of interactions among bacterial species that may lead to weakened FBIs during extreme drought. By contrast, soil fungi are shown to be more sensitive to heat than bacteria<sup>12</sup>. Asynchronous responses of fungi and bacteria to temperature or drought could potentially lead to reduced soil microbiome stability<sup>13</sup>, which we argue will ultimately depend on changes in the three types of FBI and, more importantly, how those changes feedback to each other.

## Microbial resistance and recovery

Interactions between soil fungi and bacteria determine their resistance (population or community responses during the entire period of climate extremes) against climate extremes and their subsequent recovery (population or community responses after climate extremes are over) (Fig. 2). For example, withstanding heat stress directly elevates the metabolic costs of fungi and bacteria, which could reduce hyphal exudation and the release of nutrients from bacteria, and therefore reduce cross-feeding. However, fungi may maintain or increase metabolic cross-feeding with their obligate endosymbiotic bacteria under climate extremes, even if it means a high metabolic burden. In some cases, climate extremes can break obligatory cross-feeding within and between bacterial and fungal species, thereby collapsing their population sizes. However, we still lack experimental evidence of



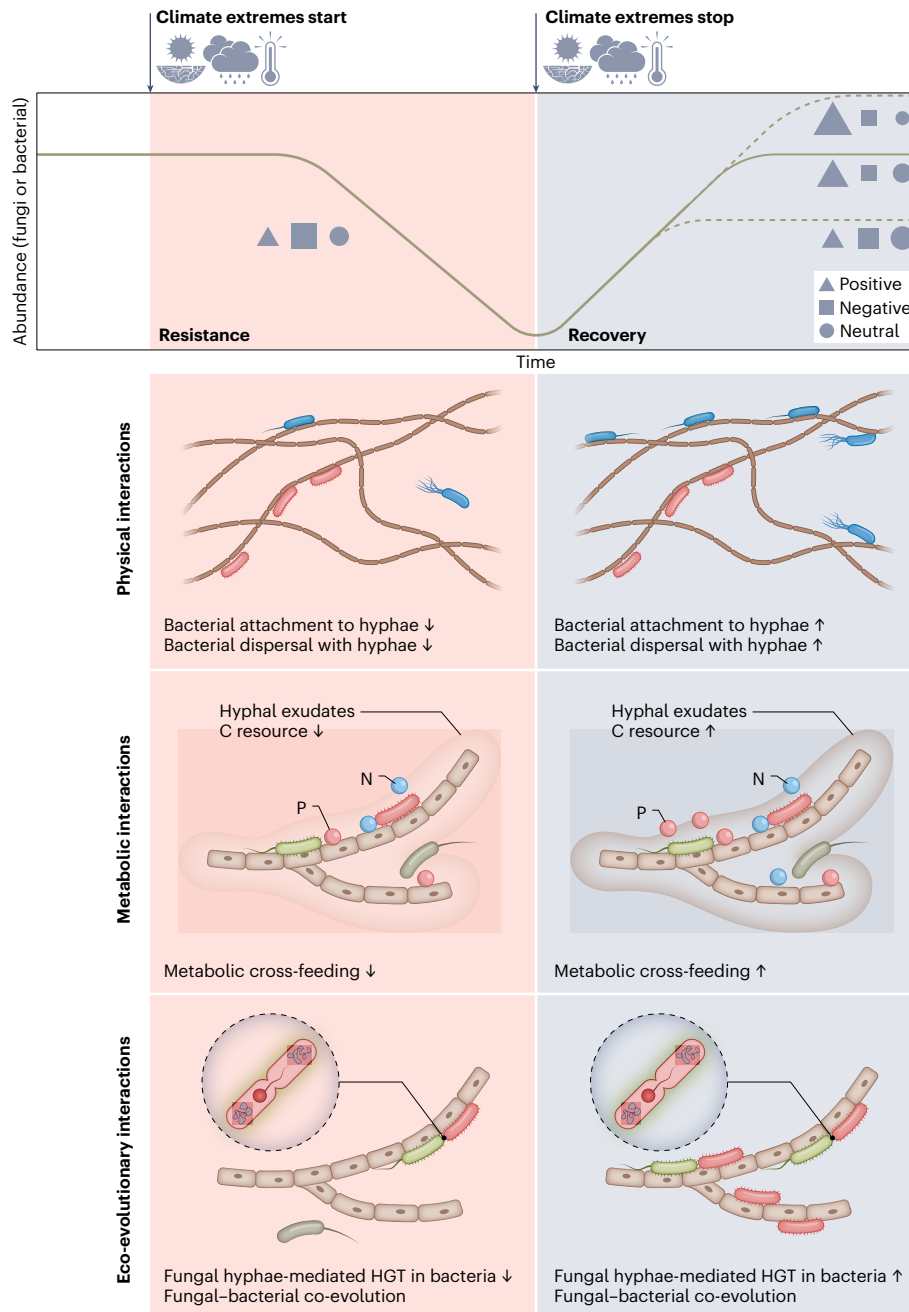
**Fig. 1 | FBIs regulate ecosystem functioning.** Interactions between fungi and bacteria broadly include physical, metabolic and eco-evolutionary interactions, which depend on one another. These interactions contribute to soil microbiome diversity and stability, which regulate various ecosystem functions. SOC, soil organic carbon. Created with [BioRender.com](https://www.biorender.com).

such breakdowns. Hyphal exudates provide easily available carbon substrates for bacterial growth and mobility<sup>4</sup>, and reduced hyphal exudation during extreme heat can weaken bacterial attachment to fungal hyphae and, thus, bacterial dispersal. Additionally, dormancy serves as an important tolerance strategy to stress, which likely reduces physical and metabolic interactions between fungi and bacteria due to decreased mobility and metabolic activities<sup>14</sup>. Reduced interactions can directly impact the eco-evolutionary interactions between fungi and bacteria. For instance, decreased hyphae-mediated HGT among bacterial cells at high temperatures may hinder bacterial adaptive evolution under temperature extremes. We suspect that a decline in FBIs would generally lead to a decline in fungal and bacterial population size during a climate extreme (Fig. 2).

Recovery after a climate extreme offers bacteria and fungi the opportunity to return to their baseline values – for example, their population size, growth rate or any other fitness-related variable, as it was before the event (Fig. 2). Understanding recovery requires knowledge of baseline values. Although baseline values for any response variables are often challenging to obtain, we consider them to be a long-term average (for example, several generation times) before a

given climate extreme event. We suggest that the different trajectories of recovery depend on the extent to which the three interaction processes were affected during the resistance phase. During the recovery phase, both fungi and bacteria can reactivate from dormant states, recover their metabolic activities and re-establish their interactions<sup>14</sup>. In this case, bacterial attachment to fungal hyphae and bacterial dispersal along hyphae will increase, and metabolic cross-feeding may also progressively increase. However, the intrinsic differences in fungal and bacterial growth rates may constrain the recovery of bacteria if fungal growth is further slowed after an extreme climate event.

The increase in hyphae-mediated bacterial HGT may facilitate the evolution of heat- or drought-tolerant bacterial species during the recovery phase. Fungi and bacteria could also enhance selection pressure and opt for microbial partners that can support each other during climate extremes. We speculate that certain types of alteration in physical, metabolic and eco-evolutionary interactions between fungi and bacteria (for example, see Fig. 2) could enhance positive interactions during recovery. This may also depend on resource availability and other environmental factors, including sequential events



**Fig. 2 | FBIs shift during the resistance and recovery phases.** Bacteria and fungi shift their interactions in various ways when exposed to climate extremes. Outlined are mechanisms related to physical, metabolic and eco-evolutionary interactions at the resistance and recovery phases of bacteria and fungi to help show how FBIs determine soil microbiome responses to climate extremes.

The downward black arrows shown for the three types of FBI during the resistance phase indicate a decline, whereas upward black arrows during the recovery phase indicate an increase. The size of shapes for positive, negative and neutral FBIs indicates magnitude. Created with [BioRender.com](https://www.biorender.com/).

that constrain full recovery<sup>15</sup>. If positive, negative and neutral FBIs return to pre-extreme event levels, then it may potentially lead to a full recovery of bacteria and/or fungi; otherwise, shifts from the baseline FBIs could lead to over-recovery or under-recovery. Variation in soil microbiome recovery post-climate extremes will eventually depend on the magnitude, frequency and duration of a given climate extreme

event to which bacteria and fungi are simultaneously exposed in different kinds of soil environments.

## Outlook

We argue that the various types of interaction between soil fungi and bacteria that would primarily determine how soil microbiomes change

to climate extremes must be acknowledged. Loss of certain interactions during climate extremes could lead to a dramatic decline in populations of fungi or bacteria, triggering the variation in recovery. A key consequence of variable recovery patterns within and between soil fungi and bacterial populations is a shift in soil microbiome community composition compared with the pre-climate extreme. The functional consequences of such shifts are still poorly understood, undermining our ability to utilize soil microbiomes in ecosystem restoration and climate change mitigation programmes. We suspect that functional shifts are tightly related to how FBIs change during climate extremes and the persistence of those changes during the recovery phase. It will require collective efforts from theoreticians and experimentalists to establish the links between FBIs and ecosystem functions to inform soil microbiome-mediated ecosystem management strategies for our sustainable planet.

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## Author contributions

J.S. and M.P.T. developed the ideas and wrote the Comment together.

## Competing interests

The authors declare no competing interests.