



Forecasting the impact of global warming on soil bacterial communities using simulated systems

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Received 8 June 2023; Received in revised form 2 October 2023; Accepted 15 March 2024

ABSTRACT

Recently, global warming has become more visible, and the entire world is experiencing its effects. Given that global temperature is rising by 0.2 °C (\pm 0.1 °C) per decade, human-induced warming reached 1 °C above pre-industrial levels around 2017 and is expected to reach 1.5 °C around 2040. However, there is a lack of comprehensive data and long-term monitoring studies on how global warming might impact the diversity of bacteria in terrestrial ecosystems. Since bacteria have a specific range of temperatures for optimal growth and metabolic activity, changes in surrounding temperature may induce a change in soil temperature, leading to alterations in the diversity and composition of soil bacterial communities. Considering the vital ecological functions performed by terrestrial soil bacteria, it is crucial to understand how terrestrial bacteria respond to elevated environmental temperatures. This knowledge will facilitate the development of appropriate intervention strategies to address the anticipated depletion of beneficial bacteria and the potential increase in pathogenic soil bacteria in the upcoming years. This review paper explores researchers' efforts over many years to document bacterial diversity and to forecast the impact of global warming on soil bacterial communities using various simulation systems. It also discusses potential mitigation strategies for preserving the pre-warming healthy soil bacteria communities.

Keywords: Bacterial diversity, global warming, open-top chamber, simulated warming, tropical soil

INTRODUCTION

Bacteria are important biological components that are essential in various functions in soils, such as the biogeochemical cycling of nutrients, improving soil structure and fertility, promoting plant growth and stress tolerance and maintaining a balanced ecosystem (Sathya *et al.*, 2016; Hartmann and Six, 2023). They break down organic matter, releasing nutrients that plants can utilize (Prasad *et al.*, 2021). Furthermore, certain bacteria produce substances that bind soil particles together, forming small aggregates that affect water movement within the soil (Hartmann and Six, 2023). Some of them can even control the spread of pathogens in soils and indirectly promote agricultural productivity (Sathya *et al.*, 2016). However, it is crucial to acknowledge the presence of pathogenic bacteria in soil, which can pose a danger to plants and potentially induce diseases. These diseases can have severe consequences, ranging from the death

of plants (Ferrareso *et al.*, 2020; Balla *et al.*, 2021) to the occurrence of diverse soilborne bacterial infections like tetanus, anthrax and botulism (Yan *et al.*, 2022). Bacterial genera, such as *Burkholderia*, *Enterobacter*, *Herbaspirillum*, *Ochrobactrum*, *Pseudomonas*, *Ralstonia*, *Staphylococcus* and *Stenotrophomonas*, can be beneficial in promoting plant growth, exhibiting antagonistic properties against plant pathogens and degrade environmental pollutants. However, they can also colonize human organs and tissues and thus cause diseases (Berg *et al.*, 2005). Given the benefits and potential risks associated with soil bacteria to the community and niche, keeping a good record of soil bacterial diversity and investigating their interactions with environmental factors such as soil fertility, soil moisture, soil pH and surrounding temperature is crucial. Understanding the intricate relationships between soil bacteria and their surrounding environment will aid in implementing appropriate measures to mitigate risks and

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preserve the beneficial contributions of these microorganisms to the community and ecosystem at large (Chin and Wong, 2020).

Among all the environmental factors, temperature is one of the major factors in determining soil bacterial diversity in an ecosystem. It has been shown that the diversity and composition of soil microbiota in tropical ecosystems were substantially associated with existing soil temperature regimes (Nottingham *et al.*, 2018). Over the years, the world has experienced a significant change in climate. Global warming has emerged as a pressing concern worldwide, which poses significant challenges to the balance of ecosystems and the species that inhabit them. In the decade 2006-2015, the increase in greenhouse gases such as methane (CH₄) and carbon dioxide (CO₂) in the atmosphere brought on by human activity induced warming up to 0.87 °C (± 0.12 °C) relative to 1850-1900 (IPCC, 2018). In 2016, the warmest global temperature on record reached 1.28 °C above the pre-industrial figure (McGrath, 2023). The Intergovernmental Panel on Climate Change (IPCC), the international body assessing the science related to climate change, stated that global warming is predicted to reach 1.5 °C above pre-industrial levels between 2030 and 2050 (IPCC, 2022), but climate scientists predict that global temperatures will continue to rise to 2.7 °C based on current government commitments to cutting greenhouse gas emissions (Stallard and Rowlatt, 2023). As global warming-induced rising surrounding temperature brings detrimental implications on the ecosystem, changes in surrounding temperature may induce a change in soil temperature, which may alter the diversity and composition of soil bacterial communities because, unlike other living organisms, bacteria are confined to specific niches and have to deal with the change.

The rise in surrounding temperature caused by increasing atmospheric CO₂ in the long term may affect the carbon balance in soils, which largely depends on the efficiency of soil microbes in accessing and using the carbon source. This may result in thermal adaptation of microbial processes and shifts in soil microbial diversity or the expression of their metabolic potential. Changes in organic acid exudation by mycorrhizal fungi as a result of the presence of CO₂ will affect the bacterial community composition, for example, the decrease in the relative abundance of oligotrophic Acidobacteria in various soils caused by elevated CO₂ (Lladó *et al.*, 2017). There is a chance that thermotolerance bacteria, which are currently in the minority in soil, will become the dominant population, displacing bacteria that are sensitive to higher temperatures (Maitra *et al.*, 2021). This will alter the current bacterial population equilibrium in the soil. The main concern is whether this change will harm agriculture or increase soil-borne human pathogens, among others. It is therefore critical to have firsthand information on the potential impacts of global warming on soil bacterial diversity as well as microbial-mediated ecological processes to develop appropriate intervention measures in the future in response to the predicted depletion of

beneficial bacteria or an increase in pathogenic bacteria (Chin and Wong, 2022).

To forecast the impact of global warming on bacterial diversity shifts in the coming decades, scientists have developed various simulation systems. These simulated models allow researchers to manipulate key environmental variables, including temperature and observe the corresponding changes in soil bacterial diversity and composition. Various researchers have used various simulation strategies in the past (Price and Waser, 2000; Emmett *et al.*, 2004; Chua and Wong, 2021), each with their own set of advantages and disadvantages, as discussed in the following sections. The results generated using these systems and some mitigation strategies for retaining beneficial soil bacteria are discussed.

GLOBAL WARMING AND ITS EFFECTS ON BACTERIAL DIVERSITY AND PLANT GROWTH

Global warming is known as a gradual increase in the average temperature of the Earth's atmosphere and oceans. This phenomenon is impacting the atmosphere as the Earth is getting warmer day by day. National Oceanic and Atmospheric Administration reported that October 2022 was the fourth-warmest October in the previous 143 years, with the global surface temperature being 1.60 °F (0.89 °C) above the average temperature of 57.1 °F (14.0 °C) in the 20th-century (NOAA National Centers for Environmental Information, 2022). The combined global land and ocean surface temperatures have gone up by 0.18 °C (0.32 °F) since 1981 and it is estimated that the temperature will keep rising by 0.2 °C per decade and may reach as high as 1 °C in 50 years (NOAA National Centers for Environmental Information, 2022).

Greenhouse gases are major contributors to global warming. Increasing global population and industrial development are some drivers causing greenhouse gas emissions, such as carbon dioxide (CO₂) and methane (CH₄). Besides, synthetic fertilizers in the agricultural industry contribute to approximately 80% growth rate of nitrous oxide (N₂O) (IPCC, 2013). These greenhouse gases trap heat, causing surrounding temperature to increase, which in the long term will affect the heat energy balance on Earth. This heat imbalance results in irreversible impacts such as biodiversity loss, land degradation, rising sea levels, increasing ground-level ozone and incline extreme weather events (IPCC, 2018). The accumulation of greenhouse gases also leads to a reduction in the yield and micronutrient concentrations of food, which will result in micronutrient malnutrition in vulnerable populations (IPCC, 2022).

An increase of 1.5 °C in global temperature was affirmed to alter the soil bacteria diversity (IPCC, 2022), as the temperature is one of the key determinants for the survival of bacteria. Different bacterial groups respond differently to warming. Some bacterial groups, such as Alphaproteobacteria, Gammaproteobacteria,

Planctomycetes and Actinobacteria are better acclimated to higher temperatures, while other bacterial groups, like Acidobacteria, Betaproteobacteria and Deltaproteobacteria experience a decrease in relative abundance as the temperature rises (Rui *et al.*, 2015). Research done by Chua and Wong (2021) showed that increases in the relative abundance of Actinobacteria and Chloroflexi were observed after twelve months of in situ OTC-simulated warming, while a significant decrease in the relative abundance of Bacteroidetes was recorded.

Since the surrounding temperature affects the soil microbial diversity, microbial-mediated ecological processes such as rates of organic matter decomposition and soil microbial respiration will be altered. Elevated global temperatures are expected to alter vegetation dynamics by interacting with physiological processes, biotic relationships and disturbance regimes (Camac *et al.*, 2015). Despite plants outcompeting soil bacteria for nutrients, mutualistic interactions between plants and microbes also occur (Meier and Bowman, 2008). Induced plant growth brought by simulated warming raised concentrations of labile carbon substrates in the soil in ombrotrophic peatlands, which then accelerated the microbial decomposition of organic waste (Bragazza *et al.*, 2013). Warming is also anticipated to increase microbial maintenance requirements to handle environmental stress (Schindlbacher *et al.*, 2011). Increases in microbial temporal turnover and major changes in the variety and patterns of functional genes in microbes have been linked to increased ambient temperature (Zhao *et al.*, 2014).

The response of soil bacterial diversity towards global warming depends on the nature of their surrounding environment. The effects are expected to be more pronounced in extreme environments such as Antarctica because most of Antarctica's surface is covered with ice, so even small changes in the mean annual temperature will result in a significant impact on the polar ecosystem and its diversity belowground (Deslippe *et al.*, 2012). Microbiota in Antarctica are mainly composed of psychrotrophic bacteria, which are expected to adapt better towards temperature fluctuations compared to other indigenous microbes such as psychrophiles (Vincent, 2010). This implies that these bacteria can adapt and grow at higher temperatures.

SIMULATED WARMING METHODS

The advent of global climate change has led to increased scientific research efforts to examine and comprehend potential effects on the biosphere of Earth (IPCC, 2013). With this, warming experiments are carried out to improve our understanding of the effects of higher temperatures at the individual, population and community scales.

Several climate models and fabricated systems are used to simulate the warming that will take place in the coming decades to forecast the potential environmental effects of rising temperatures (Hollister *et al.*, 2023). These models and fabricated systems reflect the real properties of the Earth's climate, including physical laws

like the conservation of energy and the ideal gas law. Variables such as temperature, air pressure, humidity and wind magnitude are included in the usage of climate models (Vasileva *et al.*, 2022). They are used to observe the degree of changes in the environment that may happen in the future; for example, adding greenhouse gases to the atmosphere will cause the surrounding temperature to rise. They are mainly divided into two categories, which are active and passive warming systems.

I. Active warming systems

Active warming systems involve the control of heat energy flow by using a variety of tools, for example, electrical heating cables, infrared ray lamps and growth chambers. It needs temperature monitoring to maintain constant heat differentials from the control (Aronson and McNulty, 2009).

Electrical heating cables are one of the active approaches in soil heating. They are normally used for the sprouting of crops for off-season seeds. The cables can be placed above the soil, laid on top of the soil or buried in the soil (Aronson and McNulty, 2009). They heat the soil to the requisite temperature by manipulating energy flow by directing heat transmission to the surroundings, which speeds up the germination of the seeds (Van Cleve *et al.*, 1990). This approach is rarely used in field experiments as direct heat conductance with vegetation when the cable is placed on top of the soil may affect vegetation growth. For the installation of cables in the soil, the humus or debris layer of the soil is dislodged, strongly disturbing the belowground biota, which may take several years to recover (Bergh and Linder, 1999; Aronson and McNulty, 2009). In addition, the heat dispersal of electrical heating cables is also disproportionate, where soils closer to the cable would experience more significant temperature increases (Bergh and Linder, 1999).

Infrared heaters, such as overhead infrared ray lamps, are preferable to electric heating cables for simulated warming tests with active systems. To imitate warming with the minimal impediment of sunlight, infrared lamps are positioned above the target soil area and usually in the centre of curved reflective materials, which can distribute the heat radiation evenly across the plots to simulate warming (Price and Waser, 2000). A consistent heat differential can be kept during the experiment by continuously measuring the temperatures in the experimental and control plots using a temperature monitoring system. Infrared heaters are chosen over electrical heating cables due to several advantages, such as causing minimal biological disruptions, offering the best heat dispersion and more closely mimicking the actual environmental warming process (Aronson and McNulty, 2009). Zhao *et al.* (2014) utilized an infrared heater to induce the warming of soils to examine soil microbial communities and their related soil processes in rhizospheric soil. However, infrared heaters were constrained for long-term environmental warming

investigations due to their high energy consumption, maintenance costs and complexity.

A growth chamber is another active system that can simulate warming in a controlled environment where temperature, humidity and light exposure can be manipulated (Yergeau and Kowalchuk, 2008). Differences in the abundance of soil microbes (Mateos-Rivera *et al.*, 2016), increased soil microbial respiration and increased competition between plant and soil microbes for organic and inorganic nitrogen (Chen *et al.*, 2015) have been reported. Compared to electric heating cables and infrared heaters, maintenance of growth chambers is less expensive and does not require an independent power supply since the experiment is carried out *in vitro*. Therefore, growth chambers are appropriate for the study of soil microorganisms under simulated warming, particularly for surroundings with harsh conditions like Antarctica.

The advantages of active systems are that the temperature of the experimental environment can be controlled; however, the limitations are that they cannot replicate real temperature shifts because the daily environment temperature fluctuates quite significantly at specific geographical locations, such as the polar regions in the austral summer. Furthermore, they are more expensive to run. As a result, some scientists have pursued alternative options, such as passive systems.

II. Passive warming systems

Passive systems function without external heat sources. They do not directly control energy flow and rely mainly on natural means, such as radiative heat transfer, to simulate warming (Marion *et al.*, 1997). They are generally preferred when compared to the active systems due to more affordable prices and fewer ecological impacts. Some examples of passive systems are ground cover and open-top chamber (OTC). The selection of a passive system for warming simulation relies on balancing the desired warming in the environment against undesirable environmental implications, such as overheating, light exposure and moisture changes (Marion *et al.*, 1997).

The ground cover employs infrared reflective shade covers to trap infrared radiation build-up in the soil during the day to heat underlying soil and vegetation at night (Emmett *et al.*, 2004). Plastic covers are normally used as they retain the heat of the day better at night because they are relatively thick and impermeable (Aronson and McNulty, 2009). Either black or clear plastics is applicable. Ground covers cause minor environmental alterations and require low setup costs. However, using ground cover to simulate warming has a significant disadvantage in inhibiting the rising soil temperature of treatment plots in the absence of sunlight compared to control plots (Aronson and McNulty, 2009).

Another passive approach that is helpful for simulating warmth in outdoor experiments is the open-top chamber (OTC). OTCs are hexagonal and consist of metal constructions with transparent vertical side walls that are

inwardly inclined at 60° concerning the horizontal ground surface (Cheah *et al.*, 2018). They accomplish similar functions as a greenhouse except for having an open top that reduces variations in precipitation, humidity and gaseous exchange with the external environment (Johnson *et al.*, 2013). Its warming impact is determined by the shortwave radiation from sunlight entering through the open top or the chamber's sides. Upon impact with the soil surface, the shortwave radiation is re-emitted as longwave radiation, which is reflected off within the OTC (Johnson *et al.*, 2013). The inclination improves solar radiation transmittance and heat entrapment within the chamber, causing a temperature rise of 1 °C to 2 °C inside the OTC (Camac *et al.*, 2015). As excess heat will leave the chamber through the open top via natural convection and wind-driven forced convection, the possibility of overheating is also reduced. However, there are certain limitations of OTCs as a simulated warming model, such as reduced pollinator visits and wind pollination in OTCs (Marion *et al.*, 1997). The plots should be clear to retain the OTCs in position during high winds or in situations when removal of the OTCs is necessary for specific measurements such as measurement of vegetation potential or vegetation solar spectral reflectance within the OTCs (Hollister *et al.*, 2023). Overall, minimal environmental disruption, easy deployment and low maintenance costs make OTCs a good choice for simulated warming studies (Chua and Wong, 2021; Hollister *et al.*, 2023).

III. Use of open-top chamber (OTC) as simulated warming model

Overall, the passive system has more advantages than the active system as its low operational costs to conduct and the simulated warming fluctuates following the daily temperatures while maintaining a slightly higher temperature of 1 °C to 2 °C inside the OTC, mimicking the temperatures in the coming decades. It is also more natural because the interference outside and inside the chamber are very similar, such as the amount of snow or rain received and the excretes of wildlife, such as birds and insects. Hence, OTCs are widely used to induce warming effects in field experiments worldwide. The warming impact and heat entrapment of soils inside the OTCs are validated in various studies. The difference in soil temperature between the treatment plots and control plots was between 0.81 °C to 1.15 °C (Chua and Wong, 2021), similar result is reported by Bokhorst *et al.* (2011) (0.5 °C to 1.4 °C). A study by Yergeau *et al.* (2011) recorded an average soil surface temperature of 0.7 °C inside OTC, while Camac *et al.* (2015) observed a 1.2 °C increase in average soil surface temperature. Therefore, the effectiveness of OTCs as a model to stimulate warming in soils is proven.

It is found that the sizes of OTCs affect the difference in temperature between soils inside and outside of OTCs. Ren *et al.* (2010) designed OTCs in different sizes with bottom diameters of 0.85 m, 1.15 m, 1.45 m, 1.75 m and 2.05 m. They found that the air temperature inside OTCs

increased by 2.68 °C, 1.57 °C, 1.20 °C, 1.07 °C and 0.69 °C respectively, with the increase of OTC diameter compared with ambient air (Ren *et al.*, 2010). Therefore, it can be concluded that the smaller the size of OTC, the more effective the role of OTC in simulating warming in soils.

In simulated warming experiments, a paired plot with a treatment plot adjacent to the control plot (both plots are only separated by the walls of OTC) is used to prevent high heterogeneity between plots. As soil microbial diversity is affected by various environmental factors, control plots adjacent to OTC plots are commonly included to ensure that temperature will be the only main difference between the treatment sites within the OTC and control sites outside of the OTC, with other environmental factors remaining constant.

Ren *et al.* (2010) carried out an in-situ warming experiment utilizing OTCs following the method of the International Tundra Experiment (ITEX) from November 2002 to September 2007 to examine the effects of temperature elevation on the physiological and chemical characteristics of *Elymus nutans* Griseb, a typical important plant species in the alpine meadow of Qinghai-Tibetan plateau. The result showed that increased air temperature within the range of 0.69 °C to 1.57 °C affected the physiological-biochemical characteristics of *E. nutans* on the Qinghai-Tibet plateau, which enhanced the above-ground biomass and blade height of *E. nutans* (Ren *et al.*, 2010). Thus, a rise in temperature may promote the growth and development of *E. nutans*, which may adapt and even develop defensive mechanisms in response to certain ecological changes.

Yergeau *et al.* (2011) utilized OTCs in their simulated warming experiments on soil microbial communities at different sampling sites in Antarctica. An increase in soil temperature up to 2 °C was reported, which resulted in significant increases in soil microbial abundance at every sampling site (Yergeau *et al.*, 2011). In 2014, Zhang *et al.* explored the effects of rising temperatures on the soil microbial communities in the Qinghai-Tibet Plateau using OTCs, which resulted in temperature rises of 1 °C to 1.9 °C at 0-10 cm depth. The increase in soil microbial biomass and a shift in community makeup were caused by an increase in ambient temperature (Zhao *et al.*, 2014).

On the other hand, Camac *et al.* (2015) employ OTCs to investigate the relationship between the effects of experimental warming on rates of vegetation cover change in burned and unburned alpine heathland in Australia. An increase in soil surface temperature of around 1.1 °C was reported, resulting in altered rates of change in vegetation cover (Camac *et al.*, 2015). It was hypothesized that the rising temperatures inside OTCs enhanced plant stress and caused the observed changes in vegetation cover.

Kim *et al.* (2018) also conducted passive warming experiments using OTC on the Fildes Peninsula in the maritime Antarctic. They found that the mean temperature of soil inside OTC (treatment plot) at a depth of 2-5 cm increased by approximately 0.8 °C compared to the mean

soil temperature outside OTC (control plot) with unchanged chemical and physical characteristics of soils. Total bacterial and fungal biomass of soils at the treatment plot increased by 20% compared to soils at the control plot, most probably due to increased microbial degradation activity for soil organic matter, including humic substances, resulting in the release of more low-molecular-weight growth substrates (Kim *et al.*, 2018). Hence, it has been established that rising temperatures may affect soil microbial communities in the maritime Antarctic, which would produce additional carbon sources available to other indigenous microbes.

In the study done by Zhao *et al.* (2018), the soil respiration in the experimental area of the XiaoPo Lake wetland in the Qinghai Lake Basin was simulated by simulated temperature (OTC) and natural state. The effect of warming was recorded and a rise in temperature at 1.37 °C was recorded for 5 cm-depth soil at the treatment plot compared to the control plot. An obvious increase in soil respiration rate under warming conditions was shown and the effect of precipitation on soil respiration rate was inhibited (Zhao *et al.*, 2018). This finding was supported by the study conducted by Miao *et al.* in a semiarid temperate grassland, which simulated warming using OTC significantly increased soil temperature and soil respiration by 1.48 °C ($P < 0.001$) and 42.1% ($P < 0.01$), respectively, when compared with control plots (Miao *et al.*, 2020).

Rising temperatures can result in reduced tree growth (Feeley *et al.*, 2007; Vlam *et al.*, 2014), increased tree mortality (Aleixo *et al.*, 2019) and shifting of the range of species (Khaliq *et al.*, 2014) in the tropics. A recent study by Liu and He (2022) showed that warming reduced the risk of seedling mortality of the *Ormosia semicastrata* f. *litchiifolia* (Fabaceae), a rhizobia-associated host tree species. A 3-year OTC warming experiment was done to study the plant-soil feedback on seedling mortality of several tree species and it was concluded that warming favours rhizobia-associated host tree species. Elevated temperature weakened the negative plant-soil feedback on *O. semicastrata*, as the result of a decreased relative abundance of plant-pathogenic fungi (soil pathogens) and an increased relative abundance of ectomycorrhizal fungi (soil mutualists), which influence plant performance in the tropics. This finding is supported by the study of Bachelot *et al.* (2020). Despite the temperature sensitivity of *O. semicastrata*, the rising temperature did not affect EcM fungi-associated *C. patelliformis* seedlings, as the seedlings had low susceptibility to soil-borne pathogens (Liu and He, 2022). The study highlighted the impacts of global warming on the changes in the composition of soil pathogens and soil mutualists, which will affect the mortality of tree species.

Cheah *et al.* (2018) conducted a study at Universiti Putra Malaysia using OTC to elucidate the effects of temperature increase on the soil microbes' population and the pH of the soil. The presence of a warming effect by the OTCs is proven by the increase in mean monthly and diurnal temperature. The data obtained was higher in the amount of microbial count outside the OTC. However, a

difference is clearly shown between the distribution of slow-grower and fast-grower bacteria concerning the duration of incubation time, which requires further investigation to ensure which specific group of bacteria is sensitive to the minute change due to OTC.

In addition, Chua and Wong (2021) conducted a similar study in tropical soils in Malaysia aimed at improving our understanding of the effects of rising temperatures on the composition of terrestrial bacteria in tropical soils. Although the study only lasted a year, they discovered a significant decrease in the relative abundance of Bacteroidetes and an increase in the relative abundance of Chloroflexi at the phylum level. Actinobacteria and Acidobacteria also showed changes in the relative abundance due to significant main effects of time. Significant changes in relative abundance were also observed at the genus level, where genera such as *Candidatus Koribacter*, *Candidatus Solibacter*, *Actinomadura*, *Rhodoplanes*, *Gaiella*, *Mycobacterium* and *Bacillus* spp. showed substantial changes in relative abundance over time. The outcome indicates how bacteria from soils in tropical soils will react to *in situ* warming and also acts as an early warning system for the conservation of beneficial microbes in the soil.

Despite numerous scientific efforts to forecast bacterial population shifts, the types of habitats covered are relatively limited. Many more efforts are needed to conduct similar simulated warming studies from various habitats, altitudes and countries to obtain a more representative picture of the real threat to soil bacterial populations and, thus, the soils they inhabit, particularly agricultural soils. It is challenging to develop effective strategies to mitigate the loss of beneficial bacteria from soils unless such data are available. Interestingly, many countries are already taking steps to try to delay global warming and some mitigation efforts to keep soil bacterial populations intact have been proposed.

MITIGATION OF GLOBAL WARMING

Climate change affects every corner of the world and requires international cooperation and coordinated solutions at all levels. Reducing emissions of greenhouse gases and stabilizing their atmospheric levels are important to minimize the impacts brought by climate change. Mitigation can reduce their accumulations by transitioning them to sustainable energy sources and conserving energy. Implementing the Paris Agreement is one of the actions by world leaders to work together to adapt to the current climate situation. This agreement aims to keep the global temperature increase to 2 °C (limit to 1.5 °C) above pre-industrial levels to lower the effects of climate change (Paris Agreement, 2015).

To achieve the objective of the agreement, soil plays a vital role due to its carbon-storing ability, serving as the greatest carbon sink in the environment. Biological sequestration of atmospheric CO₂ is a good approach that involves carbon capture and storage by living things

like plants and bacteria (Nogia *et al.*, 2013). It can be built either by enhancing naturally occurring carbon sequestration or by applying artificial carbon sequestration processes.

Ocean fertilization (also known as ocean nourishment) is one of the methods of biological sequestration, which helps in carbon sequestration by the phytoplanktonic photosynthesis process (Nogia *et al.*, 2013). It removes carbon dioxide levels from the ocean by introducing plant nutrients to the upper ocean to enhance marine food production and remove carbon dioxide from the atmosphere. Adding limiting nutrients, such as iron, to the ocean stimulates phytoplankton growth, which improves phytoplankton's photosynthetic ability (Yang *et al.*, 2008). The phytoplankton would fix carbon well and convert the ocean's dissolved carbon dioxide into carbohydrates. According to Wolff *et al.* (2011), iron fertilization areas had higher levels of organic matter inputs to the ocean floor, including nutrients such as polyunsaturated fatty acids and carotenoids, and there were large deep-sea species found with greater densities and biomasses but less evenly distributed. However, iron fertilization poses several risks, in which the stored organic matter may degrade and produce harmful gases such as methane and nitrous oxide that affect the ecology of the ocean (Nogia *et al.*, 2013; Yoon *et al.*, 2016; Fuss *et al.*, 2018). Besides, alterations in phytoplankton communities may affect nutrient cycling, light penetration, zooplankton grazing and organic matter accessibility to the coastal systems, which the consequences may spread to the downstream ecosystems (Scott-Buechler and Greene, 2019). So far, this effort is still on hold as it poses more risks than benefits.

Terrestrial sequestration, also called soil carbon sequestration, is storing atmospheric carbon dioxide gases in underground biomass (Nogia *et al.*, 2013). It serves as a buffer against environmental changes as it plays a vital role in regulating carbon storage and emission from terrestrial settings. Reducing deforestation and reforestation in forests, wetlands and grasslands can increase carbon sequestration as well as reduce biodiversity loss and soil degradation. By turning atmospheric carbon dioxide into environmentally friendly minerals like calcite and dolomite, soil microorganisms can eliminate atmospheric CO₂ and thus mitigate climate change (Fuss *et al.*, 2018).

Countries may undertake mitigation and adaptation strategies starting from now to manage the consequences brought by climate change. The efforts may focus on establishing policies, enacting laws, formulating, and implementing plans and programs, as well as international and regional partnerships, especially for energy, water resources, agriculture and biodiversity (Tang, 2019). Although these are long-term efforts and there are visible shortcomings in continuous improvement and monitoring, it is proven that attempts to reduce global warming will significantly benefit from understanding soil microbial diversity and their response to it.

CONCLUSION

This review paper provides an in-depth look at the major bacterial phyla found in soils. Although similar phyla dominate soils from different geographical locations, their relative abundances vary. It is also known that rising temperatures impact bacterial diversity and microbial-mediated ecological processes that may affect plant growth. The effectiveness of OTCs as a model for simulating soil warming has been demonstrated, with significant changes in the relative abundance of soil bacteria observed over time. Given the importance of soil bacteria as the major player in biogeochemical cycling and plant growth, it is of great interest to determine their responses to climate change as their changes may lead to dysfunction and disruption of the ecosystem structure.

This review paper demonstrated that the threat to bacterial diversity due to warming is real and more data is needed to develop effective strategies for retaining beneficial soil bacteria. Such simulation studies on soil bacteria are meaningful; however, they are still limited to certain geographical locations. Furthermore, the simulated warming methods used are not standardised, making it difficult to compare, for example, the data generated by an active versus a passive system. Ideally, a consortium of scientists should collaborate to harmonise methods and conduct global studies to generate enough data representing various habitats and altitudes, particularly agricultural lands. In addition, while efforts are being made to mitigate global warming, more concerted efforts should be made to conserve beneficial bacterial species and prevent the surge of pathogenic soil bacteria due to the warming.

ACKNOWLEDGEMENTS

The funding support from the Universiti Malaysia Sabah (UMS), Malaysia, under the Geran Kolaborasi Penyelidikan Dengan Institusi Luar (UMS Project Code: GKP0038-2021) is gratefully acknowledged.

REFERENCES

- Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F. et al. (2019).** Amazonian rainforest tree mortality driven by climate and functional traits. *Nature Climate Change* **9(5)**, 384-388.
- Aronson, E. L. and McNulty, S. G. (2009).** Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology* **149(11)**, 1791-1799.
- Bachelot, B., Alonso-Rodríguez, A. M., Aldrich-Wolfe, L., Cavaleri, M. A., Reed, S. C. and Wood, T. E. (2020).** Altered climate leads to positive density-dependent feedbacks in a tropical wet forest. *Global Change Biology* **26(6)**, 3417-3428.
- Balla, A., Silini, A., Cherif-Silini, H., Bouket, A. C., Moser, W. K., Nowakowska, J. A. et al. (2021).** The threat of pests and pathogens and the potential for biological control in forest ecosystems. *Forests* **12(11)**, 1579.
- Berg, G., Eberl, L. and Hartmann, A. (2005).** The rhizosphere as a reservoir for opportunistic human pathogenic bacteria. *Environmental Microbiology* **7(11)**, 1673-1685.
- Bergh, J. and Linder, S. (1999).** Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. *Global Change Biology* **5(3)**, 245-253.
- Bokhorst, S., Huiskes, A., Convey, P., Sinclair, B.J., Lebouvier, M., de Vijver, B.V. and Wall, D.H. (2011).** Microclimate impacts of passive warming methods in Antarctica: implications for climate change studies. *Polar Biology* **34**, 1421-1435.
- Bragazza, L., Parisod, J., Buttler, A. and Bardgett, R. D. (2013).** Biogeochemical plant-soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change* **3**, 273-277.
- Camac, J. S., Williams, R. J., Wahren, C. H., Jarrad, F., Hoffmann, A. A. and Vesk, P. A. (2015).** Modeling rates of life form cover change in burned and unburned alpine heathland subject to experimental warming. *Oecologia* **178(2)**, 615-628.
- Cheah, Y. K., Abdulla Seif, M., Rafi, M. I., Lim, W. M., Wong, C. M. V. L. and Tan, G. Y. A. (2018).** Effects of open-top chamber on soil chemical properties and microbial growth. *Life Sciences, Medicine and Biomedicine* **2(3)**, 2-7.
- Chen, J., Carrillo, Y., Pendall, E., Dijkstra, F. A., Evans, R. D., Morgan, J. A. et al. (2015).** Soil microbes compete strongly with plants for soil inorganic and amino acid nitrogen in a semiarid grassland exposed to elevated CO₂ and warming. *Ecosystems* **18(5)**, 867-880.
- Chin, L. M. and Wong, C. M. V. L. (2020).** Effects of elevated temperature on the tropical soil bacterial diversity. *Sains Malaysiana* **49(10)**, 2335-2344.
- Chin, L. M. and Wong, C. M. V. L. (2022).** Tropical soil bacterial diversity in Sabah, Malaysia. *Sains Malaysiana* **51(2)**, 451-460.
- Chua, C. Y. and Wong, C. M. V. L. (2021).** Effects of simulated warming on bacterial diversity and abundance in tropical soils from East Malaysia using open-top chambers. *Canadian Journal of Microbiology* **67(1)**, 64-74.
- Deslippe, J. R., Hartmann, M., Simard, S. W. and Mohn, W. W. (2012).** Long-term warming alters the composition of Arctic soil microbial communities. *FEMS Microbiology Ecology* **82(2)**, 303-315.
- Emmett, B. A., Beier, C., Estiarte, M., Tietema, A., Kristensen, H. L., Williams, D. et al. (2004).** The response of soil processes to climate change: Results from manipulation studies of shrublands across an environmental gradient. *Ecosystems* **7(6)**, 625-637.
- Feeley, K. J., Joseph Wright, S., Nur Supardi, M. N., Kassim, A. R. and Davies, S. J. (2007).** Decelerating growth in tropical forest trees. *Ecology Letters* **10(6)**, 461-469.

- Ferraresso, J., Lawton, B., Bayliss, S., Sheppard, S., Cardazzo, B., Gaze, W. et al. (2020).** Determining the prevalence, identity and possible origin of bacterial pathogens in soil. *Environmental Microbiology* **22(12)**, 5327-5340.
- Fuss, S., Lamb, W. F., Callaghan, M. W., Hilaire, J., Creutzig, F., Amann, T. et al. (2018).** Negative emissions - Part 2: Costs, potentials and side effects. *Environmental Research Letters* **13(6)**, 063002.
- Hartmann, M. and Six, J. (2023).** Soil structure and microbiome functions in agroecosystems. *Nature Reviews Earth and Environment* **4**, 4-18.
- Hollister, R. D., Elphinstone, C., Henry, G. H. R., Bjorkman, A. D., Klanderud, K., Björk, R. G. et al. (2023).** A review of open top chamber (OTC) performance across the ITEX Network. *Arctic Science* **9(2)**, 331-344.
- IPCC, Intergovernmental Panel on Climate Change. (2013).** Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T. F., Qin, D., Plattner, G., Tignor, M. M., Allen, S. K., Boschung, J. et al. (eds.). Cambridge University Press, United Kingdom and USA.
- IPCC, Intergovernmental Panel on Climate Change. (2018).** Summary for policymakers. In: Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Masson-Delmotte, V., Zhai, P., Pörtner, H., Roberts, D., Skea, J., Shukla, P. R. et al. (eds.). Cambridge University Press, UK and USA.
- IPCC, Intergovernmental Panel on Climate Change. (2022).** Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Pörtner, H., Roberts, D. C., Adams, H., Adler, C., Aldunce, P., Ali, E. et al. (eds.). Cambridge University Press, UK and USA.
- Johnson, C. P., Pypker, T. G., Hribljan, J. A. and Chimner, R. A. (2013).** Open top chambers and infrared lamps: A comparison of heating efficacy and CO₂/CH₄ dynamics in a Northern Michigan peatland. *Ecosystems* **16(5)**, 736-748.
- Khaliq, I., Hof, C., Prinzinger, R., Böhning-Gaese, K. and Pfenninger, M. (2014).** Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20141097.
- Kim, D., Park, H. J., Kim, J. H., Youn, U. J., Yang, Y. H., Casanova-Katny, A. et al. (2018).** Passive warming effect on soil microbial community and humic substance degradation in maritime Antarctic region. *Journal of Basic Microbiology* **58(6)**, 513-522.
- Liu, Y. and He, F. (2022).** Warming shifts soil microbial communities and tropical tree seedling mortality. *Ecology* **103(12)**, e3810.
- Lladó, S., López-Mondéjar, R. and Baldrian, P. (2017).** Forest soil bacteria: Diversity, involvement in ecosystem processes, and response to global change. *Microbiology and Molecular Biology Reviews* **81(2)**, e00063-16.
- Maitra, S., Pramanick, B., Dey, P., Bhadra, P., Shankar, T. and Anand, K. (2021).** Thermotolerant soil microbes and their role in mitigation of heat stress in plants. In: Soil Microbiomes for Sustainable Agriculture. Yadav, A. N. (ed.). Springer, Cham. pp. 203-242.
- Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H. et al. (1997).** Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology* **3(Suppl 1)**, 20-32.
- Mateos-Rivera, A., Yde, J. C., Wilson, B., Finster, K. W., Reigstad, L. J. and Øvreås, L. (2016).** The effect of temperature change on the microbial diversity and community structure along the chronosequence of the sub-arctic glacier forefield of Styggealdsbreen (Norway). *FEMS Microbiology Ecology* **92(4)**, fnw038.
- McGrath, M. (2023).** Global warming set to break key 1.5C limit for first time. Environment Correspondent. BBC: <https://www.bbc.com/news/science-environment-65602293>. [Retrieved on 21 July 2023].
- Meier, C. L. and Bowman, W. D. (2008).** Links between plant litter chemistry, species diversity, and below-ground ecosystem function. *Proceedings of the National Academy of Sciences of the United States of America* **105(50)**, 19780-19785.
- Miao, Y., Liu, M., Xuan, J., Xu, W., Wang, S., Miao, R. et al. (2020).** Effects of warming on soil respiration during the non-growing seasons in a semiarid temperate steppe. *Journal of Plant Ecology* **13(3)**, 288-294.
- NOAA National Centers for Environmental Information. (2022).** Monthly Global Climate Report for October 2022. National Centers for Environmental Information: <https://www.ncei.noaa.gov/access/monitoring/monthly-report/global/202210>. [Retrieved on 2 December 2022].
- Nogia, P., Sidhu, G. K., Mehrotra, R. and Mehrotra, S. (2013).** Capturing atmospheric carbon: Biological and nonbiological methods. *International Journal of Low-Carbon Technologies* **11(2)**, 266-274.
- Nottingham, A. T., Fierer, N., Turner, B. L., Whitaker, J., Ostle, N. J., McNamara, N. P. et al. (2018).** Microbes follow Humboldt: Temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes. *Ecology* **99(11)**, 2455-2466.
- Paris Agreement. (2015).** In report of the conference of the parties to the United Nations framework convention on climate change (21st session, 2015 Paris). **4(2017)**, 2.
- Prasad, S., Malav, L. C., Choudhary, J., Kannojiya, S., Kundu, M., Kumar, S. et al. (2021).** Soil microbiomes

- for healthy nutrient recycling. *In: Current Trends in Microbial Biotechnology for Sustainable Agriculture*. Yadav, A. N., Singh, J., Singh, C. and Yadav, N. (eds.). Springer, Singapore. pp. 1-21.
- Price, M. V. and Waser, N. M. (2000)**. Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications* **10(3)**, 811-823.
- Ren, F., Zhou, H., Zhao, X. Q., Han, F., Shi, L. N., Duan, J. C. et al. (2010)**. Influence of simulated warming using OTC on physiological-biochemical characteristics of *Elymus nutans* in alpine meadow on Qinghai-Tibetan plateau. *Acta Ecologica Sinica* **30(3)**, 166-171.
- Rui, J., Li, J., Wang, S., An, J., Liu, W., Lin, Q. et al. (2015)**. Responses of bacterial communities to simulated climate changes in alpine meadow soil of the Qinghai-Tibet plateau. *Applied and Environmental Microbiology* **81(17)**, 6070-6077.
- Sathya, A., Vijayabharathi, R. and Gopalakrishnan, S. (2016)**. Soil microbes: The invisible managers of soil fertility. *In: Microbial Inoculants in Sustainable Agricultural Productivity*. Singh, D., Singh, H. and Prabha, R. (eds.). Springer, India. pp. 1-16.
- Schindlbacher, A., Rodler, A., Kuffner, M., Kitzler, B., Sessitsch, A. and Zechmeister-Boltenstern, S. (2011)**. Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biology and Biochemistry* **43(7)**, 1417-1425.
- Scott-Buechler, C. M. and Greene, C. H. (2019)**. Role of the ocean in climate stabilization. *In: Bioenergy with Carbon Capture and Storage: Using Natural Resources for Sustainable Development*. Pires, J. C. M. and Gonçalves, A. L. D. C (eds.). Academic Press, United States. pp.109-130.
- Stallard, E. and Rowlett, J. (2023)**. World will miss 1.5C warming limit - Top UK expert. BBC News Climate and Science. BBC: <https://www.bbc.com/news/science-environment-66256101>. [Retrieved on 21 July 2023].
- Tang, D. K. H. (2019)**. Climate change in Malaysia: Trends, contributors, impacts, mitigation and adaptations. *Science of The Total Environment* **650(2)**, 1858-1871.
- Van Cleve, K., Hom, J. L. and Oechel, W. C. (1990)**. Responses of black spruce (*Picea mariana*) ecosystems to soil temperature modifications in Interior Alaska. *Canadian Journal of Forest Research* **20(9)**, 1530.
- Vasileva, I. L., Nemova, D. V., Vatin, N. I., Fediuk, R. S. and Karelina, M. I. (2022)**. Climate-adaptive façades with an air chamber. *Buildings* **12**, 366.
- Vincent, W. F. (2010)**. Microbial ecosystem responses to rapid climate change in the Arctic. *ISME Journal* **4(9)**, 1087-1090.
- Vlam, M., Baker, P. J., Bunyavejchewin, S. and Zuidema, P. A. (2014)**. Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. *Oecologia* **174(4)**, 1449-1461.
- Wolff, G. A., Billett, D. S. M., Bett, B. J., Holtvoeth, J., FitzGeorge-Balfour, T., Fisher, E. H. et al. (2011)**. The effects of natural iron fertilisation on deep-sea ecology: The Crozet Plateau, Southern Indian Ocean. *PLoS ONE* **6(6)**, e20697.
- Yan, Z., Xiong, C., Liu, H. and Singh, B. K. (2022)**. Sustainable agricultural practices contribute significantly to One Health. *Journal of Sustainable Agriculture and Environment* **1(3)**, 165-176.
- Yang, H., Xu, Z., Fan, M., Gupta, R., Slimane, R. B., Bland, A. E. et al. (2008)**. Progress in carbon dioxide separation and capture: A review. *Journal of Environmental Sciences* **20(1)**, 14-27.
- Yergeau, E., Bokhorst, S., Kang, S., Zhou, J., Greer, C. W., Aerts, R. et al. (2011)**. Shifts in soil microorganisms in response to warming are consistent across a range of Antarctic environments. *ISME Journal* **6(3)**, 692-702.
- Yergeau, E. and Kowalchuk, G. (2008)**. Responses of Antarctic soil microbial communities and associated functions to temperature and freeze-thaw cycle frequency. *Environmental Microbiology* **10(9)**, 2223-2235.
- Yoon, J. E., Yoo, K. C., Macdonald, A. M., Yoon, H. I., Park, K. T., Yang, E. J. et al. (2016)**. Ocean iron fertilization experiments: Past-present-future with introduction to Korean iron fertilization experiment in the Southern Ocean (KIFES) Project. *Biogeosciences* **2016**, doi:10.5194/bg-2016-472.
- Zhao, C., Zhu, L., Liang, J., Yin, H., Yin, C., Li, D. et al. (2014)**. Effects of experimental warming and nitrogen fertilization on soil microbial communities and processes of two subalpine coniferous species in Eastern Tibetan Plateau, China. *Plant and Soil* **382(1-2)**, 189-201.
- Zhao, S., Chen, K., Wu, C. and Mao, Y. (2018)**. Effects of simulated warming on soil respiration to XiaoPo lake. *IOP Conference Series: Earth and Environmental Science* **113**, 012219.