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Review

Soil microbiome as an essential player in climate change and plant health control: a review**

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A b s t r a c t. The European Union's Biodiversity Strategy for 2030 places significant emphasis on sustainable agriculture, including microbes, which play a crucial role in climate change mitigation and in supporting plant health. The strategy aims to put Europe's biodiversity on the path to recovery by 2030. Soil microbiomes are highly diverse and play a pivotal role in providing ecosystem services that support this diversity, thereby enhancing soil quality and functions such as carbon sequestration, greenhouse gas (GHG) emission mitigation, nutrient cycling, and plant disease control. This review evaluates the incidence of climate change-borne plant pathogens across the world, focusing on the importance of both heat-resistant fungi, which can be either pathogenic or beneficial, and microbiome-based solutions and their effects on soil processes and microbiome status. We explore the interactions between soil and plant microbiomes to regulate plant health, enhance plant resilience, and improve soil quality through microbial supplementation. Furthermore, we examine the necessity for soil health restoration to reverse biodiversity loss.

K e y w o r d s: biodiversity, climate change, microbiomes, soil functionality, soil health, regenerative agriculture

1. INTRODUCTION

As the world's population grows at unprecedented rates and concomitant demand on natural resources increases, humanity faces the need to live more sustainably on Earth. Finding this balance requires understanding the various facets of specific problems and their interrelationships (UNESCO, 2003). In this context, examples of real-world problems include the emerging global food crisis and issues related to soil quality and health (Lal *et al.*, 2020, 2021). The immediate food security dimensions relate to food access but also encompass regions' ability to meet their basic needs.

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Modern agriculture and horticulture face multiple challenges; they need to be more productive to meet rising food demand while also becoming more efficient in mitigating climate change and preserving the environment and human health (Zhao *et al.*, 2017). The latest report on regenerative agriculture in Europe (EASAC, 2022) emphasised the importance of restoring soil health, enhancing carbon storage, and reversing biodiversity loss. Moreover, the report underscored the critical role of microbes in maintaining soil ecology and in transforming mineral and organic soil compounds. According to Horizon Europe Mission (EC, 2020), 60-70% of EU soils are threatened mainly due to unsustainable agricultural management practices (Panagos *et al.*, 2022). Moreover, each year up to 40% of food crops are lost due to the attack and spread of plant pests (FAO, 2021). Additionally, increases in soil-borne plant pathogens pose a significant threat to the environment; in agricultural systems with already low biodiversity, this can lead to further declines in biodiversity and increased pathogen pressure (Lacroix, 2021; EASAC, 2022). Therefore, healthy soils with high biodiversity of beneficial microbiomes are key to the production of healthy, nutritious food and crucial for protecting crops against plant pests and diseases (Frąc *et al.*, 2018; Hannula *et al.*, 2020).

Research on soil microbiomes and the contribution of microbes to sustainable agricultural development has increased steadily over the last 10 years. Still, information on soil microbiome diversity, structure, mechanisms of interaction, and, especially, functions influenced by changing environmental conditions remains limited (Crotty *et al.* 2022). The main goals of this review are to summarize our knowledge of the role of the soil microbiome, especially emphasized soil fungal and bacterial microbiome as an essential driver of soil and plant health; of soil functioning under a changing climate, including soil microbiome biodiversity and functionality; and of the importance of climate change-borne plant pathogens and heat-resistant fungi, the latter of which can sometimes be beneficial. Moreover, this review provides an overview of the influence that soil microbiomes can have and the services they can provide for a climate-resilient future, including greenhouse gas emissions, soil-plant microbiome interactions, and microbially based solutions for sustainable agriculture. In addition, we give specific recommendations for the prediction of plant diseases, soil health, and quality in a changing climate. As soil microbiome stability and diversity are essential for maintaining the eubiosis state relevant to soil health and therefore to plant health, in this review, we identified major drivers, issues, challenges, and research future needs in the field of linking, networking, and relationships between soil microbiome and plant pathogens.

2. MICROBIOMES IN A CHANGING CLIMATE

To improve the ecological state of soils and enhance soil health, mitigate climate change, and strengthen food security in Europe and worldwide, innovative solutions are needed, including groundbreaking research on new agricultural practices. One approach to developing new strategies for sustainable agriculture is to explore and understand soil microbiomes as essential agents in mitigating climate change, improving soil functioning, and improving plant health.

Although a clear definition of "microbiome" is still under discussion (Marchesi and Ravel, 2015), Berg *et al.* (2020) recommended defining the soil microbiome as a characteristic microbial community inhabiting a well-defined habitat with specific physico-chemical properties. In addition, the microbiome should be considered not only as the microbes themselves but also as other components essential for their activity, such as metabolites, metabolic abilities, or proteins, which together create specific ecological niches and dynamic micro-ecosystems. According to this definition, in the soil environment, the characteristic soil microbial community, together with "*a theatre of their activity*", creates the soil microbiome. Moreover, integrative microbiomes include bacteria, archaea, fungi, protists, algae, and viruses, which are also referred to as mycobiome, protistome, virome, and even eucaryome (Geisen, 2021). Other researchers have proposed using expressions such as bacterial, archaeal, or fungal community instead (Berg *et al.*, 2020).

3. MICROBIOME BIODIVERSITY AND SOIL FUNCTIONALITY

The soil is a "tiny" place that can host a high number of different organisms, including bacteria, fungi, archaea, and protists. It is estimated that as many as 10 000-50 000 microorganisms can co-exist in one gram of soil (Chaparro *et al.*, 2012; Schloss and Handelesman, 2006). The soil microbiome is a complex ecosystem, but with advances in molecular and bioinformatics, more profound insights into its importance, roles, and shifts under different conditions and over time are becoming possible. Recent studies have provided increases in data concerning soil microbiomes in other ecosystems such as croplands (Suman *et al.*, 2022; Chen *et al.*, 2019; Frąc *et al.*, 2020), grasslands (Cao *et al.*, 2021; Vieira *et al.*, 2021; Frąc *et al.*, 2020), forests (Baldrian, 2017), wetlands (Bahram *et al.*, 2022), drylands (Coban *et al.*, 2022), and arctic areas (Taş *et al.*, 2018; Tripathi *et al.*, 2019). All these data indicate enormous microbiome biodiversity depending on climatic zone (Bona *et al.*, 2021), soil type and depth (Bona *et al.*, 2021; Mącik *et al.*, 2020a), shifts under biotic and abiotic stressors (Jansson and Hofmockel, 2020; Coleman-Derr and Tringe, 2014) and other natural, environmental, or anthropogenic factors (Hofer, 2022; Boros-Lajszner *et al.*, 2021; Zaborowska *et al.*, 2020; Islam *et al.*, 2020). The root systems of plants can influence the composition of the microbiome, as the exudates they emit can vary with plant genotype and age, as well as with soil structure, texture, pH, and fertility. Pii *et al.* (2016) found that different plant species can promote specific rhizosphere types, favouring microorganisms beneficial to their growth and protection. Moreover, they discovered that the production of root exudates not only influences the structure of the soil community but also its functions. It is essential to highlight that the root microbiome, called the rhizobiome, interacts with the (bulk) soil microbiome, and both are shaped by plant exudates, providing an exometabolite network in the soil rhizosphere (Sasse *et al.*, 2018).

Soil functionality depends on soil life, especially the abundance, diversity, and structure of the microbiome. Microorganisms, especially bacteria and fungi, are responsible for a range of soil functions, including organic matter decomposition, nutrient cycling, support of plant productivity, improvement of soil structure, and carbon sequestration, as well as suppression of soil-borne plant diseases (Coban *et al.*, 2022). Biodiversity of a soil microbiome is crucial for ecosystem services, as changes in microbial community structure can affect the functions, stability, and resilience of the system, including in the face of future disturbances (Jansson and Hofmockel, 2020). Although the mechanisms by which soil microbiomes mediate ecosystem-scale responses to climate change remain poorly characterized, it is evident that microbes respond sensitively not only to biological influences, but also to physical and chemical factors, which, when present in inappropriate concentrations or intensities, act as potent stressors (Coban *et al.*, 2022; Frąc *et al.*, 2018; Rahman *et al.*, 2021). Some authors suggest that soil functionality can be improved by managing the soil microbiome to adapt to diverse conditions, which in turn might help mitigate the negative consequences of climate change (Liu *et al.*, 2022) and facilitate the suppression of plant pathogens (Deng *et al.*, 2021). Bacteria and fungi participate in biochemical carbon transformations in the soil environment and produce carbon polymers, including polysaccharides and proteins, which, together with bacterial and fungal cells and necromass, support the formation of soil aggregates (Frąc, 2019), stabilizing and increasing carbon stocks in the soil (Jansson and Hofmockel, 2020). The study of microbiomes can be used to identify microbial consortia capable of catalyzing these reactions to enhance carbon storage in soil (Hicks *et al.*, 2017). Moreover, soil microbiomes can be manipulated *in situ* by the addition of amendments such as, for example, biochar, increasing their capacity to store carbon in the amended soil (Walkiewicz *et al.*, 2020; Kubaczyński *et al.*, 2022; Jansson and Hofmockel, 2020). Microbes can also store root exudates as stable metabolites in their biomass (Jansson *et al.*, 2018). The capacity of soil to sequester carbon is greater when soil biodiversity is higher (Lal *et al.*, 2004). These two critical elements of soil functionality, microbial biodiversity and carbon sequestration, should be supported by sustainable agricultural management practices such as intercropping, crop rotation, conservation tillage, manuring and green manuring, agroforestry, as well as application of bioproducts, biofertilizers and biopreparations (Suman *et al.*, 2022). Plant growth-promoting bacteria and fungal inoculants, or the stimulation of the microbiome by application of different amendments directly into the soil environment, can alleviate drought stress in plants (Yadav *et al.*, 2021; Pylak *et al.*, 2019; Mącik *et al.*, 2020a). There are reports of the use of plant growth-promoting bacteria not only for plant biostimulation, improving growth, quality, and fitness (Drobek *et al.*, 2020; Drobek *et al.*, 2019), but also for the mitigation of the consequences of climate change (Compant *et al.*, 2010; Coleman-Derr and Tringe, 2014). Arbuscular mycorrhizal fungi (AMF), either alone or in combination with bacterial and fungal endophytes, also enhance plant growth and vitality (Ważny *et al.*, 2022). Additionally, they can help induce plant tolerance to drought, salinity, pollution, and extreme temperatures (Kothe and Turnau, 2018). AMF can also directly increase plant water access by expansion of their mycelia into soil pores filled with water (Jansson and Hofmockel, 2020). It was suggested that mutualistic interactions between arbuscular mycorrhizal fungi and plant roots increased drought resilience by regulating glucose exudation and rhizosphere expansion (Hoang *et al.*, 2022). Finally, mycorrhizal and beneficial fungi can assist with plant nitrogen acquisition and mitigate N_2O emissions; as natural inhibitors of urease they may also contribute to blocking ammonia release from nitrogen mineral fertilizers (Pertile *et al.*, 2021; Jansson and Hofmockel, 2020). These examples of soil functionality can be applied to climate change mitigation by harnessing the beneficial properties of the soil microbiome.

To summarize, due to its complexity and diversity, the soil bacterial and fungal community can cope with various abiotic and biotic stresses if the microbial community structure is restored to a stable, more resilient soil microbiome than before disturbance (Coleman-Derr and Tringe, 2014; Mącik *et al.*, 2022). It is critical, therefore, to select and test different bioindicators to monitor the structure, diversity, and function of the community and to understand microorganisms' responses to various stresses and climate change. Given the biodiversity and soil functionality of the soil microbiome, the next looming knowledge gap concerns the *metaphenome*, defined by Jansson and Hofmockel (2018) as the expression of functions encoded in microbial genomes in combination with the environment. The metaphenome covers the whole *omics* field; the metagenome, metatranscriptome, metaproteome, and metabolome, as well as their relationship to soil microbial genomes, expressed genes, proteins, and metabolites, respectively (Jansson and Baker, 2016). However, because the soil metaphenome is affected by the soil environment, a considerable challenge remains for measuring and predicting the impacts of environmental disturbances on pivotal functions performed by soil microbiomes.

4. CLIMATE CHANGE-BORNE MICROORGANISMS ACROSS THE WORLD

Climate change can impact the range shift of microbiological contaminants and plant diseases, including microorganisms causing post-harvest loss, pathogens infecting crops, soil-born pathogens, as well as, seed-born pathogens.

A specific group of microorganisms able to take advantage of changing climatic conditions is heat-resistant fungi. Their survival and spore germination can be promoted by warmer conditions (Suryanarayanan *et al.*, 2011; Frąc *et al.*, 2015), including high air and soil temperatures and drought induced by fires (Day *et al.*, 2020). Soil microbiomes comprise heat-resistant fungi that serve multiple functions. In the soil environment, saprotrophs in particular participate in the decomposition of plant residues (Day *et al.*, 2020) as well as sequestration of carbon (Clemmensen *et al.*, 2015), and they have an essential role in the context of biodiversity restoration after wildfires (Day *et al.*, 2020; Glassman *et al.*, 2016; Birnbaum *et al.*, 2019). However, some species of heat-resistant fungi can also pose a risk to agricultural products; they are sometimes considered food contaminants due to their spoilage properties and capacity to produce mycotoxins (Pertile *et al.*, 2020; Santos *et al.*, 2018; Frąc *et al.*, 2015), which is especially relevant in organic production. They are of considerable significance to ecosystem carbon dynamics, either through the decomposition and return of carbon as a nutrient or by supporting the accumulation of carbon in plants (Day *et al.*, 2020). Increasing heat causes some fungal species to switch from yeast to filamentous forms, making them virulent and able to infect animals and plants (Leach and Cowen, 2013). It is also speculated that during past climate changes, rapid wood degradation by thermoresistant saprophytic fungi contributed to the emission of greenhouse gasses (Pieńkowski *et al.*, 2016).

Plant diseases caused by fungal pathogens are undesirable not only because they reduce yields but also because fungi often produce mycotoxins that are hazardous to human health (Brito *et al.*, 2022; Sarmast *et al.*, 2021; Fornal *et al.*, 2017). Global climate change is accelerating the dissemination of fungal pathogens into new areas (Liu *et al.* 2019; Helfer 2014). This shift is estimated to have been ~8 km polewards per year since 1960 (Bebber *et al.*, 2013). Milder winters and warmer springs and summers have led to the spread of harmful microorganisms and intensified the occurrence of fungal diseases in crops. Phytopathogens that attack plants in regions they where they have not previously been recognized cause severe damage in the agricultural sector by making it challenging to implement plant protection methods in a timely and efficient way (Fig. S1). However, the emergence of pathogens in previously non-endemic regions can also be associated with the movement of hosts, human-mediated transport pathways, and the dispersal capacities of diverse biological vectors (Jones *et al.*, 2008).

Although global trend projections for the spread of fungal pathogens associated with global warming are upward, it is essential to remember that individual fungi can increase or decrease in occurrence in particular regions. Global warming is connected not only to an increase in ambient temperature but also to changes in humidity, rainfall frequency, and even rising GHG concentrations in the atmosphere (Manabe, 2019). One of the leading causes of wheat powdery mildew, *Blumeria graminis*, is a fungus belonging to the Leotiomycetes class; it decreased at high temperatures (26 to 30°C) compared to low temperatures (18 to 22°C). Higher ambient CO_2 levels accelerated dissemination of the fungus on wheat (Slavica *et al.*, 2018; Komáromi *et al.*, 2013), oilseed (Oehme *et al.*, 2013), and zucchini (Pugliese *et al.*, 2012), but interestingly, the wheat research (Bencze *et al.*, 2013) also reported the opposite effect of CO_2 concentration on disease prevalence. Although it has been shown that increased temperature and CO_2 levels are unfavourable for some fungal pathogens, many scientists report that those microorganisms will expand their distribution areas under climate change (Chaloner *et al.*, 2021).

The rate of growth and aggressiveness of plant pathogens can also be enhanced under changing environmental conditions, leading to increased agricultural losses. *Fusarium* head blight and crown rot are caused by several *Fusarium* and *Microdochium* species. The fungi *F. graminearum*, *F. culmorum*, *F. pseudograminearum*, and *F. acuminatum* (Xu and Nicholson, 2009; Akinsanmi *et al.*, 2004) are strongly influenced by weather conditions in terms of disease severity and importance. Specifically, higher ambient temperatures and humidity are associated with increased concentrations of mycotoxins produced by these pathogens in grains (Schaafsma and Hooker, 2007). Additionally, the toxin concentration in grains produced by *Aspergillus flavus* is associated with reduced rainfall and increased temperature (Damianidis *et al.*, 2018). Another fungal pathogen, *Kabatiella caulivora*, a main fungal pathogen of subterranean clover (*Trifolium subterraneum*), caused more severe damage to its host at higher temperatures (Guerret *et al.*, 2016). Also, higher aggressiveness in *Puccinia striiformis*, which causes yellow rust of wheat, was observed at higher temperatures (10 to 18°C *vs* 12 to 28°C) among new strains (isolated post-2000 compared to pre-2000) adapted to warmer temperatures (Milus *et al.*, 2009).

Apart from adaptation of a particular pathogen to a changing climate, distribution can shift from less to more harmful microorganisms. With drier and warmer summers, infection of maize plantations in Hungary from 2009 to 2016 moved from *F. verticillioides* to *A. flavus,* resulting in increased aflatoxin contamination of grains. It is worth noting that in 2014, when the summer was cool and rainy, that toxin was not detected in the yield (Miedaner and Juroszek, 2021).

Another consideration in discussing pathogen dispersal in the context of climate change is the varying resilience of hosts under changing environmental conditions. For example, oilseed rape's resistance to *Leptosphaeria maculans* (causal agent of phoma stem canker) was expressed at 15°C but suppressed at 25°C (Huang *et al.*, 2006). Moreover, it was demonstrated that an increase in ascospore release by *L. maculans* and *L. biglobosa* was correlated with increasing temperature and precipitation (Kaczmarek *et al.*, 2016). This was irrespective of differences in the metabolic capacities of these fungi (Frąc *et al.*, 2022), confirming the substantial impact of climate change on steam canker severity in oilseed rape. In contrast, some resistance genes in rice (Webb *et al.*, 2010) and wheat (Uauy *et al.*, 2005) exhibit increased expression under higher temperatures. New pathogens of strawberry plantations in Poland, such as *Pilidium* spp., *Pestalotiopsis* spp., and *Gnomomiopsis* spp. were noted by Malarczyk *et al.* (2020); in the past, these pathogens were considered typical in warmer tropical and Mediterranean climate zones (Debode *et al.*, 2011; Karimi *et al.*, 2016; Torbati *et al.*, 2019). The five most invasive plant pathogens are increasingly dangerous. They include *Phytophthora infestans*, which attacks potatoes and tomatoes; *Hemileia vastatrix*, which causes coffee leaf rust; *Fusarium oxysporum*, which blocks the uptake of water and nutrients into the plant cells of banana; *Plasmopara viticola*, *which* causes fungal disease of grapes; and *Xylella fastidiosa* bacterium, economically crucial for several crops such as citrus, almond, peach, as well as ornamental and forestry plants (FAO, 2021). According to the literature, the above-mentioned plant pathogens can be distributed and spread because climate change creates favourable conditions for them. These include increased warming and in some regions also humid conditions, permitting pathogen accumulation earlier in the growing season (Fahim *et al.*, 2011) or reducing their incubation period (Ghini *et al.*, 2011), either of which can increase the risk of diseases caused by these pathogens. For soft-rotting bacteria such as *Pectobacterium atrosepticum*, an apparent increase in virulence was observed at 35°C (Hasegawa *et al.*, 2005). In contrast, it was found that high temperatures such as 28-32°C reduce the expression of virulence genes of *Agrobacterium* bacterial strains (Jin *et al.*, 1993). In *Pseudomonas syringae*, temperature has been shown to affect virulence, indicating that bacterial blight in soybean was observed in planta at low temperatures (Weingart *et al.*, 2004). Moreover, heat-loving plant pathogenic bacteria, which have emerged as a serious problem worldwide, belong to the bacterial species *Ralstonia solanacearum*, *Acidovorax avenae*, and *Burkholderia glumea* (Schaad 2008). The species of pectolytic bacteria associated with crop loss include *Erwinia* spp. (also known as *Pectobacterium* spp. or *Dickey* spp.) and *Clostridium*. In warmer climates, also species of the other genera may play an important role (Kůdela *et al.*, 2009).

For the future of agriculture, it is essential to consider the spread of individual fungal phytopathogens independently, as well as the incidence and proportions of fungal trophic modes in the environment. A survey covering six continents and ~73% of Earth's global environmental conditions indicated that the most critical factor driving the growth of relative pathogen incidence in ecological samples was mean annual temperature. Analyses further revealed that temperature is strongly correlated with the incidence of plant-pathogenic genera such as *Alternaria*, *Fusarium*, *Venturia*, and *Phoma*. These results were consistent with a nine-year field warming experiment, in which the team observed three times greater relative abundances of plant pathogens in soil and an increase in the frequency of occurrence of pathogenic *Cladosporium* spp. (Delgado-Baquerizo *et al.*, 2020).

Overall, global warming creates favorable conditions for the spread of fungal pathogens in many regions of the world. Dissemination of harmful microorganisms is not only directly related to climate change but also indirectly, as in warmer, drier climates, insects (which are vectors of many bacteria, fungi, and viruses) spread. Importantly, insects also feed on plants, causing wounds that provide a gateway for pathogens to enter the host organism and thrive. Likewise, with climate change, the distribution of critical crops is shifting. For example, maize is expanding northwards in Europe, which will benefit pathogens that attack plantations introduced into new areas (Miedaner and Juroszek, 2021). In addition, pathogens are constantly specializing; their temperature and host niches can be altered (Chaloner *et al.*, 2020), which, in connection with the issues listed above, create a complex web of connections affecting the spread of fungal diseases around the world and making a significant problem for plant protection in agriculture and food production. Moreover, a recent study showed the greater importance of fungal networks and trophic modes than α-diversity of the mycobiome in maintaining plant and soil health (Siegieda *et al.*, 2023). Therefore, only regular and effective monitoring of both soil and plant microbiome composition can protect us from the unexpected discovery of previously unseen pathogens that could cause severe crop losses in particular regions.

5. IMPORTANCE OF HEAT-RESISTANT FUNGI

A specific group of microorganisms that are able to take advantage of changing climatic conditions is heat-resistant fungi. Their survival and spore germination can be promoted by warmer conditions (Suryanarayanan *et al.*, 2011; Frąc *et al.*, 2015), including high air and soil temperatures and drought induced by fires (Day *et al.*, 2020).

Soil microbiomes comprise heat-resistant fungi that serve multiple functions. In the soil environment, saprotrophs in particular participate in the decomposition of plant residues (Day *et al.*, 2020) as well as sequestration of carbon (Clemmensen *et al.*, 2015), and they have an essential role in the context of biodiversity restoration after wildfires (Day *et al.*, 2020; Glassman *et al.*, 2016; Birnbaum *et al.*, 2019). However, some heat-resistant fungal species can also pose a risk to agricultural products; they are sometimes considered food contaminants due to their spoilage properties and capacity to produce mycotoxins (Pertile *et al.*, 2020; Santos *et al.*, 2018; Frąc *et al.*, 2015), which is especially relevant in organic production.

Heat-resistant fungi are highly resistant organisms that demonstrate little to no response to pressure and heat treatments (Frąc *et al.*, 2015; Panek *et al.*, 2016; Pertile *et al.*, 2020). The process by which thermo-resistance in heat-resistant molds is established is still not well enough recognized. Their ability to withstand high temperatures is currently attributed to their sexual spores, called ascospores (Piecková *et al.*, 2020). Depending on the species, they can resist from 60°C, *e.g.*, *Aspergillus niger*, *Chaetomium* spp., *Penicillium* spp., *Scytalidium lignicola* to 90°C, *e.g.*, *Neosartorya fischeri*, *Nodulisporium* sp., *Talaromyces avellaneus* (Jesenská *et al.*, 1993). In some cases (*e.g.*, *Penicillium spinulosum*), heat stimulates sporulation, meaning that pasteurization, as a treatment, might have a beneficial effect on the growth of these fungi (Sammons, 1999).

Heat-resistant moulds isolated from the soil have repeatedly been reported to contaminate pasteurized, canned, and raw fruit products (Jesenská *et al.*, 1992; Piecková *et al.*, 1994). Fungal contamination can cause severe economic losses, primarily by reducing production and fruit survival time in cold storage (Malarczyk *et al.*, 2020). Species most commonly identified as spoilage agents are *Byssochlamys* sp., *Neosartorya* sp., and *Talaromyces* sp. (Tournas, 1994; Frąc *et al.*, 2015). *N. fischeri* ascospores can contaminate heat-processed items even under microaerobic conditions. Mycotoxins excreted by these molds, *e.g.*, verruculogen and fumitremorgins, can pose a risk to public health (Frąc *et al.*, 2015; Fornal *et al.*, 2017; Pertile *et al.*, 2020). Although thermal treatment can be used to eliminate fungi, in the agricultural industry the time and temperature values required to inactivate spores often cannot be applied, as they modify the sensory, physical, and chemical characteristics of produce (Berni *et al.*, 2017).

Fungi are of considerable significance to the carbon dynamics of ecosystems, either via the decomposition and return of carbon as a nutrient, or by supporting the accumulation of carbon in plants (Day *et al.*, 2020). Thermotolerant and thermoresistant species of saprotrophic fungi include representatives of the following genera: *Agaricus*, *Aspergillus*, *Morchella*, *Mucor*, *Penicillium*, and *Rhizopus* (Gupta and Tuohy, 2019).

Increasing heat causes some fungal species to switch from yeast to filamentous forms, making them virulent and able to infect animals and plants (Leach and Cowen, 2013). It is also speculated that during past climate changes, rapid wood degradation by thermoresistant saprophytic fungi contributed to the emission of greenhouse gases (Pieńkowski *et al.*, 2016). In contrast, soil-borne fungi have been shown to increase plant drought resistance and thermotolerance. A good example is thermoresistant *Curvularia protuberata* present in Yellowstone Park. The soil of this area can reach 60°C, yet it does not affect the fungus (Redman *et al.*, 2002).

Wildfires, occurring more frequently due to increasing temperatures, also have a significant impact on soil, crops, and microecosystems. Post-fire microbial changes affect the environment in both positive and negative ways, altering the sequestration and regeneration of carbon in plants. About 40 species of fungi require fire to produce spores. Some, such as heat-resistant *Rhizopogon olivaceotinctus*, can spread more efficiently after burning (Glassman *et al.*, 2016). It is known that post-fire germination of heat-resistant fungi, such as *P. spinulosum* or *F. gracilipes*, can modify the composition of plant communities after burning, primarily by hindering conifer restoration. It has also been observed that most conifer seedlings contaminated with these fungi have lower biomass and develop more slowly. This change in plant cover, in turn, can affect soil characteristics and drive ecosystem shifts in plant composition after burning. It was found that after fire, heat-resistant fungi reduced coniferous seedling biomass, suggesting that they may play a role in structuring plant communities after burning (Day *et al.*, 2020).

Lignin peroxidases from *Pestalotiopsis palmarum* enable it to utilize heavy crude oil as its only carbon source, making it a potential tool for purifying soil used in organic farming. Chitinases isolated from *Lecanicillium muscarium* have been found to interact with insect exoskeletons, thereby increasing the effectiveness of bio-pesticides and enabling lower chemical usage in agriculture (Gupta and Tuohy, 2019).

To summarize, if appropriate monitoring of heat-resistant fungi, including their capabilities, is conducted, we can move from regarding them exclusively as dangerous microbiological contaminants of agricultural products and food to agents that assist in crop production applications. Moreover, there is a need to extend research on heat-resistant fungi to deepen our understanding of their metabolic, morphological, and genetic properties that shape their resistance to compounds used in agriculture and food processing. Preservatives, chemicals, and natural plant extracts have the potential to be used in sustainable farming as biological agents against non-beneficial microbes (Oleszek *et al.*, 2019), especially important in view of current climate change. Publications on microorganisms or their processes in subsurface soil layers account for less than 3% of articles in ecological journals, with few discussing the impacts of environmental changes (Pritchard, 2011). This aspect of soil should be explored further in future research.

6. SOIL MICROBIOME SERVICES FOR A CLIMATE-RESILIENT FUTURE

The use of soil microbiome services in strategies for soil and plant protection and restoration has received widespread attention in recent years (Fig. 1). Bioproducts based on beneficial microorganisms facilitate increases in crop yields and in environmental defence mechanisms against phytopathogens. These are valuable contributions to reducing the use of mineral fertilizers and plant protection products, such as pesticides, including herbicides and fungicides. Biological products based on microorganisms and dedicated to agriculture are termed biofertilizers, bioprotectants, biopreparations, or biostimulants (Prashar *et al.*, 2014; Martinez-Viveros *et al.*, 2010; Mącik *et al.*, 2020a; Pylak *et al.*, 2019).

The application of biofertilizers also enhances plant tolerance to various stressors, which is crucial for developing climate-resilient agriculture (Kashyap *et al.,* 2017; Adhya and Annapurna, 2018).

Microorganisms, such as plant growth-promoting bacteria (PGPB), arbuscular mycorrhizal fungi (AMF), yeasts, and actinomycetes, have the potential to support plant growth. These microbial communities have multiple strategies to increase plant growth and improve soil quality and health. The main effective mechanisms of beneficial microorganisms (which are also called effective microbes-EM) are nitrogen fixing capacity, phosphate and potassium solubilization, secretion of exopolysaccharides, production of siderophores, decomposition of organic matter, release of trace elements (Fe, Zn, Si), and biocontrol activity (production of antibiotics, lytic enzymes, antifungals agents, hormones) (Nassal *et al.*, 2018; Eltbany *et al.*, 2019; Mącik *et al.*, 2020a).

Nitrogen is the primary building block of living organisms, but plants cannot utilise atmospheric nitrogen (N_2). It is only through the activity of N_2-fixing and nitrifying microorganisms that other living organisms can obtain nitrogen in the forms of ammonium (NH_4^+) and nitrate (NO_3^-). Therefore, numerous nitrogen-fixing bacteria have been applied as biofertilizers (Kloepper and Beauchamp 1992; Höflich and Ruppel 1994).

Plant growth is also increased by the phosphate-solubilizing microbes in soil microbiomes, such as bacteria (PSB, P- P-solubilizing bacteria) (Alori *et al.*, 2017; Elias *et al.* 2016; Mącik *et al.*, 2020b) and filamentous fungi and yeast (Alori *et al.*, 2017; Pal *et al.*, 2015). These groups of microbes transform insoluble phosphates into soluble forms ($H_2PO_4^-$ and HPO_4^{2-}), which plants can then absorb (Sharma, 2011; Vijayabharathi *et al.*, 2016) using various chemical processes: exchange reactions, acidification, or chelation. Hallama *et al.* (2019, 2021, 2022) described in detail how soil microorganisms can act as hidden miners of phosphorus cycling in agricultural soils.

Potassium, a third macronutrient relevant to plant growth, occurs in soil in mineral form (90-98% of the resource), which is unavailable for plant uptake. The main

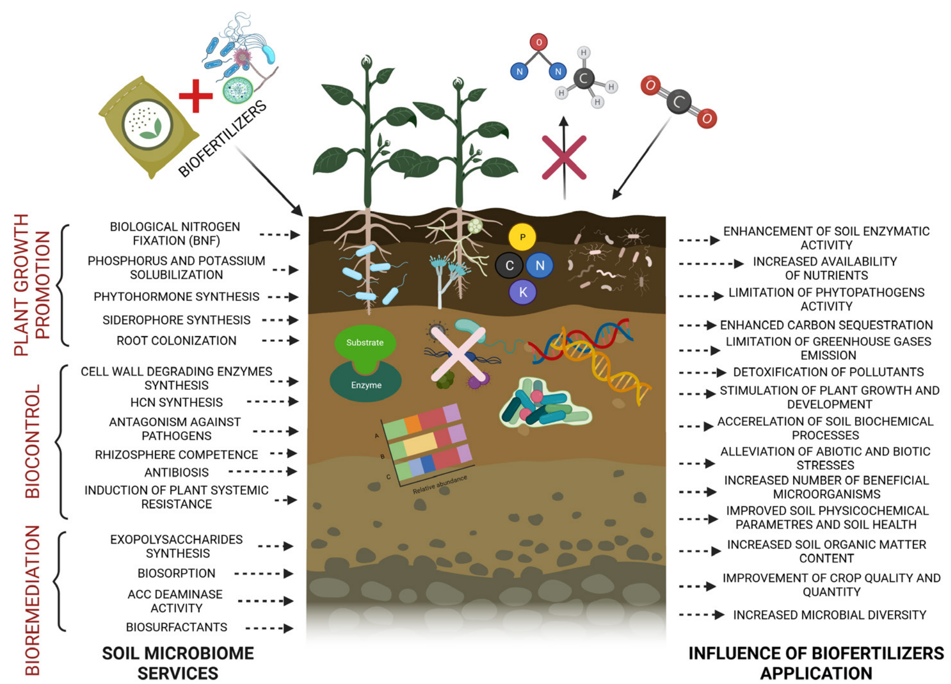

Fig. 1. Mechanisms of soil microbiome services and the responses of soil microbiomes to biofertilizer incorporation. HCN – hydrogen cyanide. Created with BioRender.com

microbial mechanisms that increase potassium availability are the production of organic acids (citric, oxalic, succinic, malic), polysaccharides, and acidolysis (Kumar *et al.,* 2018; Kumar *et al.*, 2022).

Another plant growth-promoting effect of microbes is their ability to synthesize agroactive compounds (biostimulants) such as siderophores, phytohormones, antibiotics, volatile organic compounds, exopolysaccharides, and enzymes used as biocontrol agents (Shafi *et al.,* 2017; Radhakrishnan *et al.,* 2017). These biostimulants are antagonistic to phytopathogens and can stimulate natural plant defence mechanisms. However, the inhibition of pathogen growth or its infectiousness is a synergistic effect of different mechanisms, and the number of bioactive agents involved is unknown (Hamid *et al.,* 2021). Biostimulants are also valuable agronomic tools for reducing abiotic stress (Bulgari *et al.*, 2019). Global climate change poses a challenge to biological solutions in agriculture. The application of biostimulants is reported to be an effective method for improving plant tolerance to stresses such as salinity (Fazeli-Nasab and Sayyed 2019), drought (Jochum *et al.,* 2019), heat stress (Sangiorgio *et al.,* 2020), or nutrient deficiency. Bioproducts that contain biologically active molecules improve environmental parameters by influencing primary and secondary metabolism.

Furthermore, some microbes can increase the availability of micronutrients such as Fe, Zn, or Si to plants. These elements are required in small quantities but are essential for healthy plant growth and improved crop production, especially under changing climatic conditions and a global food crisis. The mechanisms by which insoluble forms are converted have to do with the production of siderophores, organic acids, and chelating agents.

The biodegradation of plant residues and the production of soil organic matter (humus) in arable soils are key to the global carbon cycle (Ali *et al.*, 2018; Pausch *et al.*, 2018). The beneficial effects of soil microorganisms' activity on decomposition of organic wastes (organic fertilizers) are well known and described (Mahmoodabadi and Heydarpour, 2014; Gryta *et al.,* 2019; Gryta *et al.,* 2020; Zhang *et al.,* 2016). One method of controlling organic matter decomposition is the application of biopreparations. Microorganisms are often introduced during the initial decomposition stages, but they can also influence the larger microbial community, whose activity is maintained throughout the entire decomposition process. These two strategies make it possible to obtain substrate profiles that differ completely. These aspects of biopreparations improve the utilization efficiency of introduced organic wastes, the formation of organic compounds, and the formation of humus.

Although microbial inoculants can support sustainable production and help regulate climate change (Liu *et al.*, 2022), there is a knowledge gap regarding how they alter native microbial communities and their functioning. Microorganisms incorporated into the soil with carriers can clog soil pores and create hot spots with higher concentrations of microbes (Singh, 2015). Furthermore, commercially available microbial-based bioproducts may affect the autochthonic microbial populations (Radhapriya *et al.*, 2018). It is reported that geographical differences in soil microbial composition should be considered during the development of biopreparations, as microorganisms are unlikely to adapt and survive across all soil types (Coban *et al.*, 2022). Given the critical role of biopreparations, it is essential to note that a single microorganism application may not be the best strategy across a broad range of environmental conditions (O'Callaghan *et al.*, 2022). The development of multi-microbial consortia is increasingly common, and combining microorganisms with different functions can be more effective in agricultural complex ecosystems.

The other limitation of biopreparation effectiveness is stabilization of microbes during storage and application, and the adequate survival number of bacteria and fungi (Pylak *et al.,* 2023; Qiu *et al.,* 2019; Oszust *et al.*, 2021). As mentioned above, many groups of microorganisms can establish soil functions, *e.g*., nitrogen fixation, phosphorus solubilization, and organic matter transformation. However, the microbial-based biopreparations are almost always numerically disadvantaged. As it is known, microbial products typically contain 10^9 cfu per g or per ml of bioproducts, providing a total 1 x 10^{11} bacteria per ha when applied at about 1 kg ha^{-1}. By comparison, soil rhizobial communities often exceed 1000 rhizobia per g of soil (Farquharson and Ballard, 2010) equating 10^{12} rhizobia per ha. Therefore, the application strategy for bioproducts, including the incorporation of microbials at high concentrations near plant roots, is crucial for their effectiveness (O'Callaghan *et al.*, 2022). The safety knowledge of soil microbial inoculant products varies widely, due to significant differences in the regulation of biofertilizers. There is growing awareness of the need to protect soil microbial diversity. We can observe increasing biosecurity concerns around the movement of microorganisms across borders and the stimulation of plant invasions (Ricciardi *et al.*, 2017). Therefore, the introduction of microbial inoculants into new ecosystems is increasingly essential for monitoring. Bioinoculants containing large numbers of diverse, unnamed, and uncharacterized microorganisms should raise concern, as the release of alien species poses a risk of disrupting ecological integrity (Qiu *et al.*, 2019).

However, the limitations of biofertilizer and bioproduct applications are considered one of the most critical challenges in this area. Novel microbial-based biopreparations are currently being developed and tested; however, the long-term effects of these on soil properties and entire microbial communities remain to be studied. Before upscaling microbial-based approaches, detailed studies are needed in which microorganisms are enriched into living soil and long-term effects on soil microbial communities and other soil properties are tracked.

7. GHG EMISSIONS IN AGRICULTURE

Soil microbiomes play a significant role in the most important biogeochemical cycles directly involved with climate change (Naylor *et al.*, 2020), including the C and N cycles. The former is directly involved in the production of CO_2 and CH_4, while the latter is engaged in the production of N_2O. The functional genes involved in these two cycles are already used to study the effects of abiotic stresses on microbial communities (Castellano-Hinojosa *et al.*, 2018; Karas *et al.*, 2018; Levy-Booth *et al.*, 2014; Pertile *et al.*, 2021; Staley *et al.*, 2018; Suciu *et al.*, 2019; Vasileiadis *et al.*, 2018).

As bacterial functional genes are better known than those of fungi, this chapter focuses mainly on bacterial functional genes. Examples of functional genes involved in C and N cycling are presented in Table 1. The genes encoding chitinase (*chi*A, *chi*B, *chi*C) are crucial in carbon cycling, as the enzyme chitinase plays a key role in the degradation of chitin to chitobiose. Simultaneously with this step, C- and N-rich byproducts are released and can be incorporated into microbial biomass or mineralized. In contrast, the functional genes encoding bacterial CO_2 fixation (*cbb*RL) and bacterial CH_4 oxidation (*pmo*A) are used by soil microorganisms to store C, removing from the atmosphere two important gases that affect the climate and human health.

The structure and biodiversity of the soil microbiome is key to determining which path they will take; the microorganisms decide whether the carbon inside the soil is transformed into CO_2 and CH_4 or retained in the soil (Crowther *et al.*, 2016; Jansson and Hofmockel, 2018). The nitrogen cycle is a cascade process in which specific steps are linked and therefore a greater number of functional genes participate in this process. In the nitrogen cycle, the gas connected to climate change is N_2O. This gas can be produced at the end of the nitrification step (from NH_2OH reduction) or as the penultimate step of denitrification (NO to N_2O); in fact, nitrification is the key process in the production of this gas, with emissions of 30% of N_2O from the soil by nitrifier denitrification. The functional gene *amo*A is widely used in molecular microbiology as a marker to study effects on nitrification, as this group is susceptible to external disturbances (Karas *et al.*, 2018; Pertile *et al.*, 2021) and because if its abundance is low it leads to limitation of the development of the entire N cycle (Levy-Booth *et al.*, 2014). To limit emission of this harmful gas during nitrification we must increase the abundance of ammonia-oxidising archaea (AOA) compared to ammonia-oxidizing bacteria (AOB) because the N_2O/NO_2^- ratio is higher in AOB than AOA (Bakken and Frostegård, 2017).

Briones *et al.* (2002) and Bremer *et al.* (2007) observed that different plant species can influence the abundance of ammonia-oxidising bacteria (AOB) and denitrifiers. The four functional genes involved in denitrification (*nar*G, *nir*S, *nir*K, *nos*Z) are equally important, as the presence or absence of one of these genes determines whether or not the next step in denitrification is taken (NO_3^- [*nar*G] NO_2^- [*nir*S/*nir*K] NO [*nos*Z] N_2). It is essential to compare the

Table 1. Examples of functional genes involved in C and N cycling

Cycle	Gene	Enzyme	Step	Reference
Carbon	*cht*	Bacterial chitinase	Conversion of chitin to chitobiose and liberation of C and N	Ikeda *et al*., 2007; Lindsay *et al*., 2010
	*cbb*LR	Bacterial RuBisCO	Fixation CO_2 *via* Calvin-Benson-Bassham cycle	Selesi *et al*., 2007, 2005
	*pmo*A	Bacterial methane monooxygenase (pMMO)	Conversion of CH_4 to methanol	Lin *et al*., 2004
Nitrogen	*amo*A	Archaeal ammonia monooxigenase	Conversion of ammonia to NH_2OH	Francis *et al*., 2005
		Bacterial ammonia monooxigenase	Conversion of ammonia to NH_2OH	Rotthauwe *et al*., 1997
	*nar*G	Nitrate reductase	Reduction of nitrate to nitrite	Bru *et al*., 2007
	*nir*K *nir*S	Nitrite reductas	Reduction of nitrite to nitric oxide	Henry *et al*., 2004 Kandeler *et al*., 2006
	*nos*Z	Nitrous oxide reductase	Reduction of nitrous oxide to dinitrogen	Henry *et al*., 2006

N_2O/NO_2^- ratio with the abundance ratio of *nir/nosZ* genes, as the two products mentioned above are produced by the expression of these two functional genes (Bakken and Frostegård, 2017).

Agriculture depletes soil nutrients and carbon; their supply is essential for maintaining soil fertility. The use of organic fertilizers increases soil organic matter content (SOM), improves soil structure, enhances soil water retention, permeability, and root elongation, and improves the utilization efficiency of rainfall, thus improving plant growth (Wang *et al.*, 2016). Organic amendments can improve soil carbon sequestration on agricultural land (Minasny *et al.*, 2017; Bolinder *et al.*, 2020). Wildfires, occurring more frequently due to increasing temperatures, also have a great impact on soil, crops, and microecosystems. Post-fire microbial changes affect the environment in both positive and negative ways, altering carbon sequestration and/or regeneration of plants (Glassman *et al.*, 2016).

Since nutrient availability in soil from organic fertilizers occurs during mineralization, the nutrients released are likely to be synchronized with plant nutrient requirements, compared with inorganic fertilizers, thereby suppressing NO_3-N leaching and N_2O emissions (Nagatake *et al.*, 2018). In paddy fields, the return of rice straw to the soil is widely recommended to maintain and improve soil fertility and rice yield; however, concerns exist about increased CH_4 emissions (Naser *et al.*, 2007). The application of organic matter in paddy fields has been found to increase the soil's methane production potential, methane oxidation potential, and the abundance of methanogens and methanotrophs. However, proper combinations of green manure and rice straw can maintain rice yields and reduce methane production (Zhou *et al.*, 2020).

Since organic fertilizers have low short-term fertilizer effects and the nutrient balance is not easily adjusted, they can be used in combination with mineral fertilizers. However, as SOM increases, the amount of mineral fertilizer can be reduced. The effects of supplemental organic fertilizer application on crop growth and greenhouse gas emissions using three organic fertilizers (manure, slurry, and digestive liquid applied such that the amount of NPK did not exceed the recommended application rate, and shortages were supplemented with chemical fertilizers) were assessed for three years in a managed grassland in an Andosol in southern Hokkaido (Kitamura *et al.*, 2021). The amount of N from mineral fertilizer in organic fertilizer treatments decreased by 10% under manure, 19.7% under slurry, and 29.7% under digestive liquid compared with mineral fertilizer alone; grass biomass yield was not significantly different among fertilizer treatments. The main effect on the reduction of greenhouse gas emissions was due to the input of organic carbon from organic fertilizers. N_2O emissions were reduced in manure and digestate relative to mineral fertilizers, but increased in slurry (Kitamura *et al.*, 2021). This difference among organic fertilizers may be related to the progress of NO_2^- reduction. Another study found that the *nirK* gene was highest in mineral fertilizer + pig slurry and lowest in mineral fertilizer + manure (Yang *et al.*, 2022). This suggests that higher soil NO_3 concentrations lead to increased N_2O emissions. It has also been shown that continuous manure application enables sufficient crop production without mineral fertilizer supplementation, resulting in significantly lower N_2O emissions than with mineral fertilizers alone (Jin *et al.*, 2010). Appropriate continuous use of manure also helps suppress the decrease in pH caused by nitrification of NH_4. Annual N_2O emissions measured in a grassland-cornfield rotation field for 11 years were significantly negatively correlated with soil pH when nitrogen fertilizer was applied to fields with soil pH less than 6, with or without manure application (Mukumbuta *et al.*, 2017). Incubation experiments with the field soil found no N_2O release when soils were limed to a pH above 7 (Mukumbuta *et al.*, 2018). N_2O emissions at low pH were considered due to the *nosZ* gene-missing genus *Pseudomonas* (Nie *et al.*, 2016). Moreover, Pertile *et al.* (2021) indicated that after application of urea mineral fertilizer enriched with beneficial fungal strains, copies of *cbbLR* and *pmoA* genes, encoding the large subunits of the ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) and the β-subunit of the particulate methane monooxygenase (pMMO) respectively, were higher in comparison to the control soil treated only with mineral fertilizers, suggesting carbon storage by soil microbiomes.

Organic farming may contribute to the reduction of GHG emissions through decreased use of chemicals and fertilizers and increased soil carbon sequestration (Smith *et al.*, 2019). However, conventional production systems can also improve their environmental performance by adopting agricultural management practices that increase soil organic carbon storage (Venkat, 2012). Croplands are estimated to be the largest biospheric source of carbon loss to the atmosphere in Europe each year (Soussana *et al.*, 2004), driven by soil tillage, which increases greenhouse gas emissions. However, spring soil tillage reduces C mineralization compared to autumn tillage (Borgen and Hylen, 2013). In contrast, grasslands have been found to store C (Vleeshouwers and Verhagen, 2002); it is essential to note that converting grassland to cropland destroys soil carbon (Soussana *et al.*, 2004). Results from cropland- and grassland-specific models that quantify the effects of climate change on agricultural systems in Europe indicate a heterogeneous temporal and spatial trend. Both grasslands and croplands have the potential to sink carbon. However, the potential is greater in grasslands, and croplands require appropriate practices, such as crop residue management, cover crops (Carozzi *et al.*, 2022), or legume intercropping (Wang *et al.*, 2021).

To limit greenhouse gas emissions, it is necessary to test different agricultural management practices, consider plant species and diversity, and safeguard the soil microbial community, as it is closely, albeit indirectly, involved in their emissions.

8. CONCLUSIONS AND FUTURE DIRECTIONS

To improve soil health, mitigate climate change, and enhance food security in Europe and worldwide, innovative solutions are needed, including groundbreaking research on new agricultural practices. One approach to developing new strategies for sustainable agriculture is to explore and understand agroecosystem microbiomes as key agents in monitoring plant quality and health, mitigating climate change, and enhancing soil services. The importance of the microbiome for soil functions and properties cannot be underestimated. Much progress has been made in recent years in characterizing and deciphering the organization and activities of the microbiome and the value of biodiversity. However, much remains unclear and requires further research. The potential of soil microbiomes to provide ecosystem services and improve soil health and quality, as well as their essential role in soil functioning and plant health under changing climate conditions, has been documented and constructively criticised in this review.

It is essential to emphasise that the literature demonstrates both the impact of climate change disturbances on soil microbiomes and their simultaneous provision of services to enhance ecosystem health and mitigate climate change effects. As the critical role of soil microbiomes is increasingly understood, it may be used to predict climate-borne plant diseases, improve soil health and quality, and mitigate the negative impacts of climate change.

Finally, considering the challenges facing modern and future agriculture, it is necessary to focus on revolutionary approaches and solutions to climate and sustainability problems, as well as food production and security, including plant health defences. The demand for local food production is growing due to concerns about climate change and the need to reduce carbon footprints.

Authors' contributions. All authors have participated in a) conception and design of the review article; b) drafting the article or revising it critically for important intellectual content; c) approval of the final version.

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