Trends in
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Review

Partner or perish: tree microbiomes and climate change

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Understanding the complex relationships between plants, their microbiomes, and environmental changes is crucial for improving growth and survival, especially for long-lived tree species. Trees, like other plants, maintain close associations with a multitude of microorganisms on and within their tissues, forming a 'holobiont'. However, a comprehensive framework for detailed tree–microbiome dynamics, and the implications for climate adaptation, is currently lacking. This review identifies gaps in the existing literature, emphasizing the need for more research to explore the coevolution of the holobiont and the full extent of climate change impact on tree growth and survival. Advancing our knowledge of plant–microbial interactions presents opportunities to enhance tree adaptability and mitigate adverse impacts of climate changes on trees.

Highlights

Trees, as long-lived, sessile, and slowly evolving organisms, are disproportionally impacted by the impacts of climate change.

Gradual and ongoing selective pressures over extended geologic timescales has provided coevolutionary opportunity for both the tree and its microbiome (holobiont) to improve tree fitness under changing conditions. This coevolution of the holobiont could infer phenological plasticity to trees to adapt to rapid climate shifts expected in the Anthropocene.

Systems-based approaches founded on complex systems sciences, holobiome theory, combined with an understanding of coevolutionary history and application of suitable model systems will expose more opportunities to manipulate the holobiont and help us to grow climate-resilient trees and forests.

Trees are stranded from climate change

Environmental change brought about through the disruption of Earth's climatic systems is altering the habitats of plants faster than they can adapt or migrate [1]. This is putting the future of Earth's forests at risk. Relative to humans, plants have had an extremely long geologic time in which to establish microbial associations (Figure 1) [2–4]. During this natural history, frequent and prolonged exposure to changes has allowed for the development and evolution of microbiome associations that enhance fitness, survival, and the capacity to adapt to new environments [5]. This has been true for *Pinus radiata* (15 million years) as well as for human evolution (3.5 million years). Based on climate change predictions, the extent and rate of change within just a couple of life spans of *P. radiata* will exceed that recorded in recent geologic history. Long-lived species such as trees are particularly vulnerable to serious and harmful changes in the world's weather patterns (e.g., climate breakdown). They cannot shift to more favorable habitats, adapt, nor evolve at 'decadal rates' concomitant with those of climate change. Consequently, many trees are, or will be, stranded in locations where the climate has shifted beyond their normal tolerances. This argument suggests microbial associations have been essential in increasing fitness during historic periods of environmental change and can therefore be used to protect trees into the future [3,6]. The tree's microbiome enables phenotypic plasticity, enhancing its resilience amidst the challenges of the global climate crisis.

It has been proposed that long-lived species can extend or alter their phenotype through associations with microorganisms [7]. Indeed, tree–microbe relationships are already recognized as important for conferring traits necessary to tree survival, including enhanced access to nutrients, pathogen protection, and growth promotion [8]. These characteristics become increasingly important under stressful conditions [9] and, as such, the influence of the relationships between trees and their microbes amplifies with climate change. However, to fully understand this potential, the traditional understanding of the microbiome and plant as separate entities needs to be revised to instead embrace the combined expression of both the plant and its microbiome as the **holobiome** (see Glossary) and **holobiont**. The concept of the holobiont is an expanding area of research but

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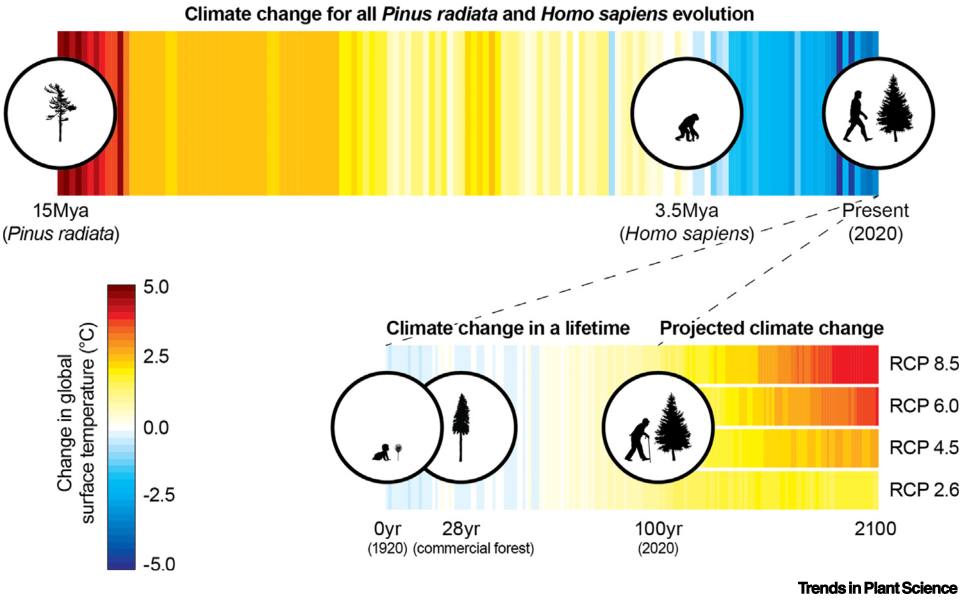

Figure 1. Historic evolutionary time versus the conifer *Pinus radiata* and *Homo sapiens* evolutionary history. The change in temperature range is compared to the period 1850–1990. The projected climate change from 2020 to 2100 is based off the IPCCs fifth Assessment Report, using representative concentration pathways (RCP) on which various scenarios in climate change are generated [4]. The RCPs are based on carbon concentrations, representing only a small proportion of the drivers for temperature providing a more conservative view on predicted temperatures.

has produced limited knowledge when related to perennial plants, in particular trees [10]. It has been proposed that long-lived species like trees may be able to adapt, extend, or alter their phylotype through associations with microorganisms. Indeed, tree–microbe relationships are recognized as important for conferring traits necessary to tree survival, including access to otherwise inaccessible nutrients, pathogen protection, and growth promotion [8]. As these characteristics become increasingly important under stressful conditions [9], the relationships between trees and their microbes will increase with ongoing climate change. However, to fully understand this potential, we need to move beyond the current understanding of the microbiome and plant as separate entities and instead embrace the combined expression of both the plant and its microbiome as the holobiome and holobiont. While the concept of the holobiont is an expanding area of research, its understanding in relation to perennial plants, in particular trees, is limited [10].

This review discusses the knowledge surrounding the microbial communities associated with trees and advocates for the use of the holobiont or holobiome approach to understand the response to climate change. The use of a complex systems approach for preserving the holobiont is encouraged to achieve and maintain our biological diversity of plant life.

Climate change and plant ecosystems: the future is not what it used to be

Much of the biotic and abiotic conditions on Earth have been formed through a long history of minor and major geophysical disturbances. These disturbances, such as successive cycles of glaciation and inter-glacial periods, have led to extreme periods of both cold and warm temperatures. Furthermore, tectonic reshaping of continents and landforms has permanently shaped the topography of Earth, building mountains, altering sea levels, and driving weathering and erosion that underpin soil formation. As a whole, these processes have contracted, expanded, and modified Hutchinsonian niche space, driving evolution of biological diversity [11]. These forces of nature are inexorable; they have, and continue to occur, over time frames concomitant to geologic change.

Glossary

Holobiome: the holobiome can be viewed as the genomic reflection of the complex network of symbiotic interactions that link an individual of a given taxon with its associated microbiome.

Holobiont: this is an assemblage of a host and many other species living in and around it, which together forms a discrete ecological unit through symbiosis.

Hologenome: the collective genetic information of an organism and the associated microorganisms (such as bacteria) that live in or on it. It reflects the idea that an organism's traits and health can be influenced by both its own genes and the genes of its associated microorganisms.

Interactome: the complete set of interactions between molecules (such as proteins or genes) within a biological system, which provides insight into how these components work together in a complex network.

Local adaptation: a population of organisms evolves specific traits or characteristics that make them better suited to the unique conditions of their particular local environment.

Phenological sensitivity: how responsive or reactive a plant is to changes in environmental cues, like temperature, which can influence its life cycle events.

Phyllosphere: the ecosystem on the surface of plant leaves, including the microbes that live there.

Rhizosphere: the narrow region of soil that surrounds and is influenced by the roots of plants. It is a place where interactions between roots, microorganisms, and the soil environment play a crucial role in plant growth and health.

Over the last decades, the world has entered the Anthropocene, a new geologic Epoch defined by the dominating influence of human activity on Earth's systems [12]. A key feature of the Anthropocene is that changes to Earth's atmosphere, hydrosphere, and biosphere are occurring at a pace not seen before (i.e., the 'Great Acceleration') [13]. Thus, while abiotic type disturbances, such as cyclones/hurricanes and droughts, and biotic type disturbances, such as disease outbreaks, have always been an integral and natural part of ecosystem dynamics [14], the alteration in the rate of occurrence of these regimes (frequency, severity, or types) can exceed the ecological tolerance of systems. Consequently, entire ecosystems, the life they support, and services they provide, are under threat. With changes in climate occurring in the Anthropocene, the future will not be what it used to be [15].

The impacts of climate change in the Anthropocene vary disproportionately across species and biomes. These differences are related to species characteristics including physiological (e.g., respiration acclimation and phenotypic change), ecological (e.g., capacity to range shift), and evolutionary response rate (e.g., the rate of acquiring new traits and/or genes), and extent of symbiont dependence (e.g., flowering time and pollinator availability) [16,17]. Terrestrial biomes at greatest risk of climate change include the grasslands and savannahs of Africa and India, tundra on the Tibetan plateau, and forests extending from the boreal north (Canada/Russia) to equatorial rainforests (the Amazon) [18]. However, the impact of climate change on trees and forested ecosystems is particularly notable. A third of Earth's habitable land is forested [19], thereby holding significant and irreplaceable biodiversity. Forest ecosystems support a myriad of services essential for planetary health and society, including providing food, medicinal, and forest products, regulating the hydrologic cycle, protecting soil resources, recreational uses, spiritual needs, and esthetic values [20]. Forests are also vital tools for mitigating the drivers of climate change. They store ~45% of terrestrial carbon, sustain the hydrologic cycle through evapotranspiration, and temper the effect of surface albedo on planetary warming due to their low albedo [21].

Impacts of climate change on forest ecosystems are already evident. In the Sierra Nevada region of California, for example, recent modeling work suggests 19.5% of modern coniferous forests in the region are occupying regions that are climatically unsuitable [22]. In many areas, tree phenology (seasonality of events such as flowering, bud burst, and fruiting) is changing in ways that disrupt pollinators [23,24]. Additionally, alterations in the frequency and intensity of abiotic disturbances, such as wind and fire events, and biotic disturbances, such as forest pest and pathogens, are having further impacts [25–27].

Such disequilibrium between vegetation and the climate is expected to be a key driver of major vegetation changes, particularly when impacting groups of species such as trees, which typically comprise 'ecosystem engineers' (i.e., have an outsized role in shaping ecosystems compared with their abundance) [28]. Paleoecological records demonstrate this has occurred extensively in the past [29,30]. Current observations and modeling expect vegetation changes to be increasingly prevalent now and into the future [31]. A key outcome of climate-altered ecosystems is the tipping point where vegetative changes can manifest as transitions of vegetation type [32]. Given the complexity in dynamics between vegetation change and climate, it is difficult to predict the timing of such tipping points; however, they represent non-linear and irreversible transitions in biome composition and functioning [33].

Tree species are particularly vulnerable to climate-related extirpation; they are long-lived, often have slow reproduction rates, and are sessile [34,35]. Natural processes of evolutionary change and range shift employed by other plant species will not work with trees, leaving local and regional populations reliant on existing genetic diversity and plasticity for site adaptation to the effects of climate change [16,17]. Other processes for trees to survive the effect of climate change are more reliant on human intervention, such as assisted migration and managed restoration through selection of 'climate tolerant traits' in breeding trials [36–38]. However, these processes, to evaluate the long-term response across breeding regimes of multiple generations using assisted migration, are complicated [36,39]. These complications include assessing how site-specific conditions might impact tree growth factors, including the susceptibility (and ultimately possible amplification) to local pathogens in the environment [36,39,40]. New approaches and new thinking must be applied for the protection and management of existing and future native and planted forests.

Microbiomes matter

Microbiomes comprise the assemblage of bacteria, fungi, oomycetes, archaea, viruses, and other microscopic organisms living on and in a defined habitat [41]. Microbial associations with higher organisms are ubiquitous and the importance of the microbiome in affecting survival and reproduction of the host has been widely demonstrated [42–44]. These microbes are dynamic and their relationships with hosts can change rapidly in response to the environment, such that some relationships may result in increased plant success under some conditions while the same set of microbes may result in decreased plant success under other conditions [45]. For example, *Cryptostroma corticales*, the causative agent of sooty bark disease, can change its lifestyle from saprotrophic species into a parasitic stage induced through water stress such as drought [46]. Much of this groundwork was laid during the human microbiome project (HMP) [47]. Initially aimed at mapping the microbial associations present on a human, the HMP found the microbiome influences human function, metabolism, physiology, and fitness, often in entirely unexpected ways. For example, gut microbes communicate to the brain and central nervous systems (nervous, endocrine, and immune signaling) [48] and these associations underlie the pathogenesis and pathophysiology of conditions ranging from irritable bowel syndrome to psychiatric and neurologic disorders (the 'brain-gut-microbiome axis') [49]. Furthermore, exposure to environmental microbiomes early in life, such as through outdoor play or interaction with pets and other animals, helps establish developmental trajectories of the immune system (the 'microbial hygiene hypothesis') [50]. The generation of data and development of new knowledge has been a key outcome of the HMP. Yet perhaps just as importantly, the HMP has changed our basic perceptions about ourselves. Our self-portrait is now one of a coalescence of human and microbial cells, where the emergent outcome of the interaction between microbiomes and human cells impacts our development, wellbeing, and many other outcomes.

Like humans, each plant species lives in close partnership with unique assemblages of microbial species (i.e., plant microbiome) [51]. However, while *Homo sapiens* have had just a few million years to form microbial associations, many plant species have had tens to hundreds of millions of years of coevolutionary opportunity [2,3,52]. This extended geologic time is important as it is set within a context of continual changes in environmental conditions. This establishes both opportunity (time) and motive (continual ecological change) for selection of plant–microbiome associations following exposure to environmental pressures. However, a key question remains: 'can plant microbiome associations established against a background of long-term environmental change enable survival into a rapidly shifting future?'.

Plant microbiomes

Microbial associations are intrinsic to plant health and fitness [51]. Interactions between plants and microbes in and on their tissues or in the environment have been documented to provide a multitude of benefits to the plant, including regulation of immunity to disease [53–55], expansion of their metabolic repertoire (secondary metabolites, volatile organic compounds, hormones), and acquisition of essential nutrients [56]. However, these microbial associations do not always stay beneficial and the dynamic nature of the microbiome can lead to alterations in the relationship between microbes and hosts (e.g., opportunistic and latent fungal pathogens *Armillaria gallica* [57] and *Sphaeropsis sapinea*) [58]. Plant microbial associations also play a pivotal role in environmental sensing, response, and adaptation to stressors by strategically influencing signal processes and perturbing, regulating, or modifying the **interactome**, particularly in the **phyllosphere** and root tissues [59]. In particular, both leaf and root surfaces are 'open systems' exposed to and connected with the surrounding environment. This extensive sensor network encompasses both above- and below-ground environments, enabling plants to detect and react to environmental changes through their microbial associations, underscoring the significant role of microbial partners in environmental monitoring and response.

The root microbiome is important for shaping plant responses to environmental stressors, including nutrient and water acquisition, protection against pests and pathogens, and phytochromes for growth and phenology. For example, on the roots, microbial aquaporin regulation influences and controls hydraulic conductance, stomatal conductance, and leaf water potential [60]. Trees often display larger root systems and higher soil microbial diversity in response to the larger niche habitats that exist throughout their larger root structure [61]. Above-ground, the global phyllosphere is estimated to cover an area of ~10^8 to 10^9 km^2 in size [62,63], which is approximately twice Earth's global surface, serving as a direct interface connecting plants and the environment. The phyllosphere is also a microbially-rich environment, holding some 10^{24} to 10^{26} microbial cells [64]. Thus, microbial activity on both the **rhizosphere** and phyllosphere impact plant water transpiration and drought response. These microbes play a pivotal role in structuring plant responses to perturbations in environmental conditions. For instance, physiological processes such as stomatal opening are influenced by phyllosphere microbial activity, thereby impacting water transpiration and drought response and gas exchange between the plant and atmosphere [63]. The reliance on the microbiome becomes more imperative to trees as the plants grow for extended periods of time where evolution is not completed to pass onto progeny within the timeframe of environmental change [65]. Tree species become reliant on the microbiome to provide these additional traits to survive the changing environment with a more rapid ability than relying on plant evolution, to transfer new traits. This allows plants to undertake physiological, ecological, and evolutionary adaptations through the assistance of their microbiome. Establishing and maintaining mutualistic microbiome symbioses that enable early detection and responses to environmental changes, or extending the reach of sensing into the environment, provide distinct competitive advantages to the plant. The microbiome itself comprises a novel source of signaling molecules that compliment and expand the range produced by the plant *per se* [66]. Thus, microbiomes can extend the plants' innate repertoire of detection capabilities for abiotic or biotic stresses, increasing the suite of environmental changes against which plants can respond. Although it remains unknown if such activity is partly or entirely outsourced to microbes, findings thus far are unveiling a central role of the plant microbiome for sensing and responding to perturbations in the environment.

To capitalize on these benefits, we are now integrating plant–microbial interactions into modern agricultural practices either by indirectly interfering in the way plants select their microbial partners or by directly stimulating or inhibiting microbial activity. One way agricultural practices have a healthy microbiome is through sustainable practices such as the use of organic amendments and/or crop rotations, which increase the phylogenetic richness, diversity, and bacterial heterogeneity of the soil when compared with soils from conventionally farmed systems [67]. Farming practitioners have also instituted the use of microbial inoculants ('bioinoculants'), whereby microbes thought to benefit plants are introduced directly to the above- or below-ground system.

Introduced microbes can support plant growth through biocontrol by providing protection against pests and pathogens, through biofertilization by increasing supply and access to nutrients, or act as biostimulators by inducing the release of phytohormones [68]. Consequently, microbiomes in agricultural systems have been used to provide benefits such as yield stability and production sustainability [69,70], disease control [71,72], and enhanced trait expression [73,74]. However, this area is still in its infancy and some bioinoculants have resulted in indirect decreased plant performance from changes to the resident soil diversity [75]. Caution is needed as not all effects of bioinoculants are positive and it is unclear if they persist or may displace other beneficial microorganisms present in the soil or associated with the plant [75].

Given the recognition of the importance of microbiomes for tree fitness, spanning nutrient acquisition through to disease protection, it is possible to employ strategies for the management of plant microbiomes in forest systems. Examples of these practices include establishment with beneficial microbes in a nursery setting before planting out, such as inoculating with beneficial ectomycorrhizal fungi [76]. Knowledge advancement, engagement, and ultimately exploitation of plant microbiomes will be required for mitigating global change in forest settings. The interactions and outcomes of phytobiome associations are profound. Like the HMP, unveiling these has reframed our understanding of what plants are, how they function, their (co)evolutionary history, and their environmental associations and phenotypic plasticity.

The holobiont and coevolution

An important consequence of microbiome studies on various host systems has been the recognition that it is typically not about the plant nor the microbiome *per se*, but the emergent outcome of the association that is important (i.e., the holobiont and its **hologenome**) [77]. This reframing is important, as it recenters our focus away from ‘a host with a microbiome’ towards a view on the meta-organism and the interactions occurring among the plant and microbial cells and the extent of their combined genetic material (mega-genome). Their fitness and success outcomes are shared. In this framework, both plants and their microbiomes (including their genetic material) collectively determine the holobiome phenome, function, and resultant ecosystem processes [78]. This makes the holobiont concept pre-eminent [79], ensuring genetic variations arising within the holobiont (particularly the microbiome) are potential sources of genomic variation that can benefit an entire collection of trees [10,78,80,81]. These neo-Darwinian concepts represent a modern scientific synthesis of coevolutionary outcomes driving ecosystem functioning. Reimagining the existing concept of a ‘tree’ from a single sessile organism with limited ability for environmental response, into a node within a holobiont network that is interacting with other nodes (trees) and collectively interacting with the environment, is pivotal in redefining how we predict climate change responses [82]. Importantly, it opens new ecological and evolutionary theory for microbiomes based on the ‘metacommunity’, potentially providing a framework for approaching any plant-dominated ecosystem. We propose that coupling this metacommunity concept with complex systems science [71] will comprise a powerful framework to explore and provide improved understanding from a holistic view and is explained further in the future recommendation section.

Traditional perspectives for species interactions consider evolutionary theory from the view of either the host, the microbiome, or a single host and single microbe. A holobiont perspective can instead open evolutionary theory to consider processes that act on the entire holobiont as a distinct unit, driving variations in the genomes of the host and the microbiome (the hologenome) [10]. Coevolution is a reciprocal genetic change in the host and symbiont following selective pressures on one another and can occur within a holobiome, where both the host and microbiome might evolve in response to the same environmental pressures, allowing the holobiome to develop and alter in response [79,83]. For the microbiome, this is more commonly referred to as diffuse coevolution, where the reciprocal evolutionary responses occur between suites of species [84]. Coevolution may not involve all members of a microbiome and could disproportionately affect highly interactive microbial taxa [85]. These microorganisms can rapidly increase as a function of local conditions, creating the equivalent of gene amplification at the species level [10]. Studying the hologenome, coexpression, co-metabolomics, and phenotypes is an approach to better understand coevolution [86,87].

The rate of both ecological and evolutionary response and subsequent evolution of the holobiont is an important but overlooked factor in predicting climate change impacts on perennial plants [17]. When climate change causes species loss, there are opportunities for novel interactions to arise [87,88], the robustness of which is dependent on the arrival of horizontally transmitted microbes to support a stable functional compositional state. If we consider the holobiont as an element of selection in evolution, then cooperation between the microbiota and the host generally leads to improved fitness for both the tree host and the microbes. Exploring species interactions that modulate evolutionary responses to climate change is an area that has been highlighted previously as needing further investigation [86,87]. However, key knowledge gaps remain, including the rate of trait evolution and horizontal gene transfer in response to stress disturbance (i.e., climate change). We also have little understanding of magnitude, if any, that extension of phenotypic traits is transferred from microbiomes to host. Addressing these gaps will require advancements in conceptual and technical analytical frameworks.

Phenological sensitivity to a changing climate

Trees can survive in changing environments through physiological, ecological, and evolutionary based adaptative mechanisms [89] that increase their fitness and reproductive success. Generally, the ecological and evolutionary adaptations of trees take centuries to millennia to occur because of their (oftentimes) slow rate to reach reproductive maturity; it is inevitable that the suitability of plants for their habitat will decrease as climate change is accelerating at a rate that far exceeds their ability to adapt or evolve (**phenological sensitivity**). Long-lived trees may overcome this limitation through their relationship with biotic factors, which can act as strong selective pressures since they affect an organism's fitness through the ability of individuals to contribute descendants to subsequent generations in their local environment [89–94]. As previously discussed, microbes in particular may be important for this role due to their fast replication rates, horizontal gene transfers, and rapid dispersal ability across the globe [95]. These factors have been particularly important in driving adaptation of populations to their local environment (i.e., **local adaptation**) and can result in coevolution between microbes and their host such that they drive genetic change in one another. Being able to understand the coevolution between plants and their microbes is essential to fully understand local adaptation of trees to their environment [89–94]. The microbiome may transfer some phenotypes to the host (Rúa and Hoeksema, under review), but transferring traits (genes) to a host is not well documented. Thus, despite a plethora of studies examining plant–microbe adaptation, we are yet to see direct evidence for coevolution and the transfer of new traits to hosts for trees and their microbes [83]. The limitations around this may reflect difficulties in experimental manipulations with long-lived species and/or a lack of theoretical basis for how the microbiome can transfer its traits to plants (Rúa and Hoeksema, under review).

Viewing microbiomes, holobiomes, and holobionts through complex systems science

By their nature, holobionts inherently comprise complex systems. The plant and microbiome together form an ecological unit interacting with the environment [96]. Such complexity can lead to unexpected and idiosyncratic outcomes. This is particularly evident for the holobiont: the hyper diversity in species and functionality of the microbiome, interacting in a network of different above- and below-ground tissues via cascades of chemical signaling and ecological interactions, in reciprocal interaction and feedback with the environment. All the primary components of complex systems are fundamental to holobiomes: agents, interactions, networks, emergence, adaption, and feedback loops.

It is clearly unfeasible to predict the emergence of phenotypic changes in the holobiome, for example, enhancement of climate resilience attributes, based on behaviors of individual components. Rather, the complexity of the system necessitates that approaches inherently based on the entire attributes of the system (as before) be used. Indeed, if our goal is to advance our understanding of the holobiome towards increasing resilience of trees to climate change, approaches grounded on the inherent characteristics of the system are needed. This is especially critical when considering the variability of the environmental context (changing climate) against which the emergent expression of the holobiome must be formally considered. Complex systems science provides a valuable lens through which we can understand and potentially manipulate these emergent phenotypic outcomes, arising from intricate interactions. The foundation of complex systems science rests on the principle that global dynamics are not readily predicted from individual behaviors; they emerge from the local interactions of entities within the system. Hence, adopting an approach grounded in complex systems may unveil novel insights into the interplay between the host, microbiome, and environment. This is particularly important when considering investigation of long-lived species such as trees within the socio-ecological systems associated with climate change [97].

Approaches based on complex systems theory have been applied across a wide range of domains spanning physics, computer sciences, through to sociology. However, the transdisciplinary framework applied to these areas is underpinned by a shared series of principals, including heterogeneity, hierarchy, self-organization, openness, adaptation, memory, non-linearity, and uncertainty [98]. When applied to microbiome ecology and holobionts, in particular, they are composed of diverse microbial species (agents) with different functions, interactions, and feedback loops among themselves (microbiome), the host, and a changing environment. Heterogeneity in the microbial community is expected to lead to complex, emergent behaviors and dynamics within the holobiont itself, let alone expression of outcomes across the holobiont and environment. Approaches that embody ‘systems within systems’ complexity and integrate scalability are essential.

Another key characteristic of complex systems is hierarchical organization. For instance, there is a hierarchy of interactions, from individual microorganisms to microbial communities to the host organism itself, each with its own set of rules and dynamics. Holobionts often exhibit self-organizing properties where the interactions among the host and its microbiota lead to emergent patterns and functional outcomes. Self-organization can contribute to the stability and resilience of the holobiont but remain grounded in ecological processes driving community assembly and turnover (priority effects, dysbiosis, ecological drift, and so forth).

Holobionts are open systems, meaning they exchange matter and energy with their environment. Indeed, this exchange with the environment is foundational to holobiont's dynamics and ability to respond, adapt, and evolve to changing conditions [99]. Holobionts can exhibit ‘memory’ in the sense that they can retain information about past environmental conditions such as drought or temperature, which, in turn, can influence responses to future challenges [100]. Microbial communities can display adaptive responses to specific stimuli or conditions they have previously encountered [96].

Interactions within holobionts are often non-linear, meaning that small changes in one component can lead to disproportionate and unexpected effects in other components [101]. As such, direct projection of influences of microbiome change on holobiont function are unreliable, resulting in high uncertainty in predicting their behavior and responses to environmental changes [102]. This uncertainty highlights the critical need for appropriate and robust modeling techniques underpinned by appropriate data. In this context, the establishment of model tree–microbiome systems becomes paramount, enabling research to investigate the complex interactions that predict responses to environmental changes.

Viewing microbiomes and holobiomes through the shared interacting components of complex systems can improve our understanding of how their responses will be shaped with environmental, biological, and social changes and, therefore, comprehension of the intricate dynamics of these systems (Figure 2).

Concluding remarks and future perspectives

Plant–microbial interactions are complex, but increased understanding of these interactions offers huge potential and the ability to mitigate negative climate change effects for the tree host (see Outstanding questions). It is understood that the symbiotic relationship between plants and microbes is a dynamic coevolving relationship that drives a plethora of host functions. If short-lived plant species have evolved mechanisms to shape the assembly of their microbiomes from the environment, it is reasonable to expect that these processes are even more pronounced in long-lived species. As the duration of environmental exposure increases, the risk and reward associated with establishing sufficiently functional microbiomes also rise. For trees, which are exposed to and engaged with their environment for decades to centuries, this concept intuitively

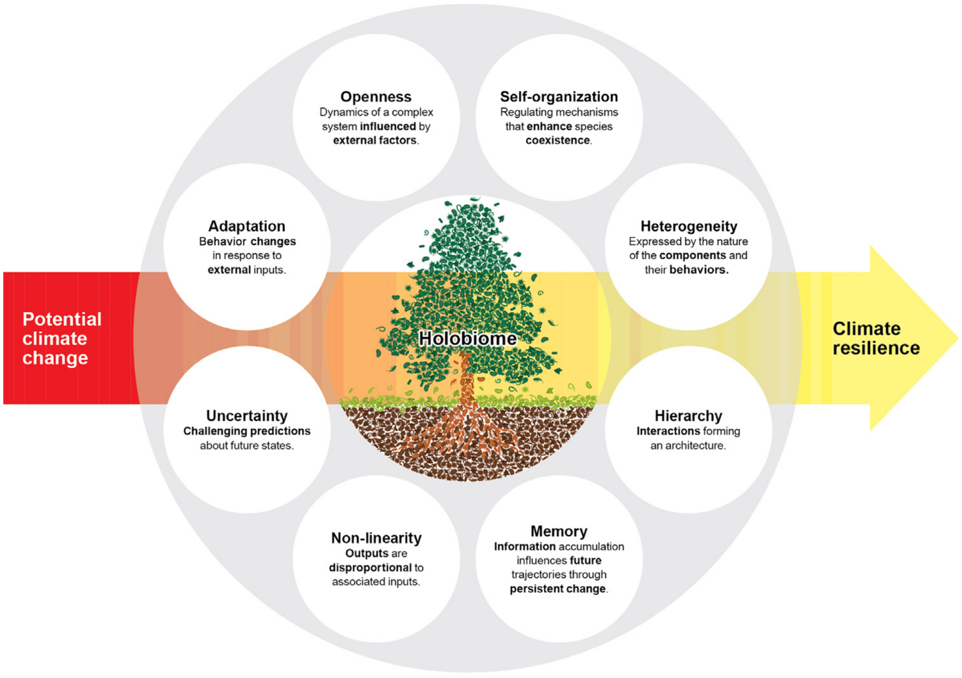

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Figure 2. Conceptual framework using complex systems science for improving understanding of how the tree hologenome can be leveraged for climate resilience.

Outstanding questions

Will plant–microbiome relationships formed in the context of persistent environmental alterations support survival in a swiftly changing future?

To what extent do plant-associated microbiomes contribute to expanding a plant's ability to detect and respond to abiotic and biotic environmental stresses, and to what degree is this detection and response capability outsourced to microbes?

Does the microbiome provide the avenue for phenotypic plasticity in trees?

Is it possible to leverage the holobiont (the combination of the plant and its microbiome) as a means to enhance our comprehension of a tree's resilience in the face of evolving environmental circumstances?

Could an enhanced knowledge of the coevolution of the holobiont be the path towards preserving biodiversity and ecosystem functions in our forests?

Can a holobiont perspective be used to open evolutionary theory for processes that can act on the entire holobiont distinct unit that then drive variations for the hologenome?

What are the specific species interactions that influence and modulate the evolutionary responses to climate change, and how do these interactions contribute to or hinder adaptation and survival in changing environmental conditions?

How does the rate of trait evolution and the occurrence of horizontal gene transfer vary in response to environmental disturbances and what implications does this have for the adaptive potential and resilience of species and ecosystems?

makes sense and significant impact of annual and long-lived plant 'lifestyles' on root microbiome assembly has been described [103]. Focused research studies directly supporting this idea are limited and more model systems are required that represent the diversity of tree species.

Significant microbiome projects, including the human microbiome, have expanded the knowledge surrounding microbiomes and the intricate and critical roles they play in human and soil health [104]. The same is needed for global tree microbiome studies, where consideration of the holobiont in forest communities has only recently been identified as an area requiring attention [78,105]. Studying tree holobiomes in the environment with a complex systems framework will allow better understanding of the interactions that occur within the environment and the driving force behind changes within the holobiont.

There is still much that needs to be studied about the mechanistic understanding on ecological and host-mediated processes that govern microbial colonization of trees, especially in the challenge of climate change. Understanding the coevolution of trees and microbiomes linked with abiotic factors could be an area that creates improved understanding of the assembly of microbiomes and their intricate relationships. Unexplored questions remain concerning what adaptations are provided by the plant–microbiome relationship to equip the tree for future growth, how the environment affects this mutualistic relationship for long-lived tree species, and how these microbiomes are transferred through generations.

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Declaration of interests

The authors declare no competing interests.

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