Plant–microbiome relations as a holobiont: critical perspectives from botany

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Abstract. The plant holobiont concept has emerged as a transformative framework in plant biology, redefining plants as integrated ecological units composed of the host and its associated microbiota. This mini-review critically evaluates the theoretical and functional implications of plant–microbiome interactions from a botanical perspective. We examine the extent to which the holobiont and hologenome concepts challenge traditional organism-centered evolutionary paradigms, with particular attention to levels of selection, co-evolutionary dynamics, and microbiome heritability. Empirical evidence demonstrates that plant-associated microbiota play fundamental roles in nutrient acquisition, growth regulation, disease resistance, and abiotic stress tolerance, positioning plant fitness as an emergent property of host–microbe interactions. However, the dynamic and context-dependent nature of microbiome assembly—driven by host selection, environmental filtering, and mixed transmission modes—raises important limitations regarding the consistency and evolutionary coherence of holobionts. While tightly integrated and vertically transmitted symbioses may approximate units of selection, most plant microbiomes exhibit partial stability and high variability, supporting the continued relevance of multi-level selection theory. Additionally, microbiome-mediated plasticity provides a rapid adaptive mechanism that can buffer environmental stress and influence evolutionary trajectories. The review also explores applied perspectives, including microbiome engineering and its potential for sustainable agriculture, while highlighting current methodological and conceptual challenges. Overall, the plant holobiont framework is best understood as a complementary, context-dependent extension of existing evolutionary theory rather than a paradigm shift.

Keywords: plant holobiont, plant microbiome, hologenome, co-evolution, microbiome assembly, ecological filtering, abiotic stress tolerance, microbiome plasticity, plant–microbe interactions.

Introduction. Over the past two decades, advances in microbiology, molecular ecology, and high-throughput sequencing have fundamentally reshaped our understanding of plant biology. Plants are no longer viewed as autonomous, genetically self-contained organisms, but rather as complex, integrated ecological units intimately associated with diverse microbial communities (García et al., 2020). This conceptual transition has given rise to the notion of the plant holobiont, defined as the host plant together with its associated microbiota—including bacteria, fungi, archaea, protists, and viruses—functioning as a biologically interconnected system (Son et al., 2026).

This paradigm shift challenges traditional organism-centric perspectives in evolutionary biology and ecology (Petrescu-Mag, 2006). Classical frameworks have typically treated the plant as the primary unit of selection, with microbial interactions considered secondary or environmental modifiers (Păpuc & Bora, 2023). In contrast, the holobiont perspective emphasizes that plant phenotype, fitness, and adaptive capacity emerge from the dynamic interplay between host genetic traits and microbiome composition (Sayyed & Ilyas, 2024). Consequently, key biological processes—such as nutrient acquisition, growth regulation, stress tolerance, and disease resistance—must be understood as co-produced by both plant and microbial partners.

At the core of this framework lies the concept of the hologenome, which encompasses the combined genetic information of the host and its microbiota (Biget et al., 2023). This integrated genomic entity introduces new theoretical questions regarding levels of selection, heritability, and co-evolution. While some scholars argue that holobionts can act as units of selection under specific conditions—particularly when microbial partners are vertically transmitted and tightly integrated—others maintain that established evolutionary models, including multi-level selection theory and co-evolutionary dynamics, remain sufficient to explain plant–microbiome interactions.

A critical feature of plant holobionts is their dynamic nature. Microbiome composition is shaped by a combination of host-driven selection mechanisms—such as immune signaling and root exudation—and external environmental filters (Ma et al., 2024). As a result, plant-associated microbial communities exhibit both stability (through conserved core microbiota) and flexibility (through environmentally acquired taxa). This duality enables rapid ecological responsiveness, allowing plants to adjust to fluctuating environmental conditions without requiring immediate genomic adaptation.

In this context, the holobiont framework provides a powerful lens through which to reinterpret plant adaptation, resilience, and evolutionary trajectories (Weckwerth et al 2025). However, it also raises important conceptual and methodological challenges, particularly concerning the extent to which holobionts function as coherent evolutionary units and how their emergent properties can be experimentally and theoretically characterized.

The aim of this mini-review is to critically evaluate the plant holobiont concept from a botanical perspective, with particular emphasis on its implications for plant fitness, evolutionary theory, and microbiome-mediated stress responses, while also exploring emerging directions that extend beyond current conceptual and empirical frameworks.

Conceptualizing the Plant Holobiont and Levels of Selection. The hologenome theory proposes that host plus microbiota, with their combined genomes (the hologenome), can act as a level of selection in evolution (Rosenberg & Zilber-Rosenberg, 2018; Zilber-Rosenberg & Rosenberg, 2008; Rosenberg & Zilber-Rosenberg, 2016; Roughgarden et al., 2018; Hassani et al., 2018). Multicellular organisms are portrayed as holobionts that function anatomically, metabolically, immunologically and developmentally as integrated entities (Rosenberg & Zilber-Rosenberg, 2016; Rosenberg & Zilber-Rosenberg, 2018; Roughgarden et al., 2018). For plants, holobiont thinking emphasizes that fitness reflects both plant genotype and its microbiota, with core microbial components transmitted across generations and more dynamic fractions renewed from the environment (Zilber-Rosenberg & Rosenberg, 2008; Rosenberg & Zilber-Rosenberg, 2016; Rosenberg & Zilber-Rosenberg, 2018; Hassani et al., 2018).

However, broader evolutionary analyses argue that existing frameworks focusing on individuals and interacting lineages are generally sufficient; holobionts can be treated as interacting entities without requiring a new evolutionary paradigm (Koskella & Bergelson, 2020; Hawkes et al., 2020). Microbiome dynamics, partial heritability, and strong environmental filtering question how often holobionts meet strict criteria as primary units of selection, especially when many community members are transient (Koskella & Bergelson, 2020; Hassani et al., 2018).

Holobiont Functions and Plant Fitness. Plant-associated microbiota influence growth, nutrient acquisition, stress tolerance, disease resistance and survival, making plant fitness an emergent outcome of host and microbiota together (Ullah et al., 2025; Vandenkoornhuyse et al., 2015; Suman et al., 2022; Gopal & Gupta, 2016; Trivedi et al., 2020). Microbiomes contribute to plant performance by supplying nutrients, modulating hormones (e.g. auxin), shaping root architecture, protecting from pathogens, and enhancing tolerance to abiotic stress (Mesny et al., 2023; Singh et al., 2023; Tan et al., 2021; Vandenkoornhuyse et al., 2015; Suman et al., 2022; Gopal & Gupta, 2016; Trivedi et al., 2020).

Host plants, in turn, shape microbiome assembly via immune signaling, cell wall properties and exudates that recruit beneficial taxa, while microbe–microbe interactions (competition, mutualism) further structure communities (Mesny et al., 2023; Vandenkoornhuyse et al., 2015; Hassani et al., 2018; Trivedi et al., 2020). Experimental work with *Lemna minor* shows that microbiome presence and rapid evolution of a single member (*Pseudomonas fluorescens*) can either increase or decrease multigenerational host fitness depending on evolved biofilm traits and associated changes in hormone production (Tan et al., 2021).

Table 1

Main plant fitness components influenced by microbiomes

Fitness component / function	*Microbiome contributions in plants*	*References*
Growth and productivity	Promotion of biomass, flowering, yield via nutrient mobilization, phytohormones	Singh et al., 2023; Tan et al., 2021; Suman et al., 2022; Gopal & Gupta, 2016; Trivedi et al., 2020
Nutrient acquisition	Mineralization, delivery of N, P and other nutrients; "second genome" functions	Vandenkoornhuyse et al., 2015; Suman et al., 2022; Gopal & Gupta, 2016; Trivedi et al., 2020
Disease resistance	Suppression of pathogens via antagonism, induced resistance, community buffering	Mesny et al., 2023; Vandenkoornhuyse et al., 2015; Suman et al., 2022; Gopal & Gupta, 2016; Trivedi et al., 2020
Abiotic stress tolerance	Mitigation of drought, salinity, heat, metals via multiple biochemical routes	Singh et al., 2023; Ullah et al., 2025; Iqbal et al., 2023; Ma et al., 2020; Suman et al., 2022; Muhammad et al., 2024.

At the holobiont scale, these contributions can shift selective pressures on plant traits; by buffering stress, microbiomes may relax or redirect selection on plant-intrinsic tolerance and defense mechanisms (Hawkes et al., 2020).

Microbiome Assembly, Transmission, and Ecological Filtering in Plant Holobionts. A central aspect of understanding plant holobionts lies in elucidating how microbial communities are assembled, maintained, and transmitted across spatial and temporal scales (Vandenkoornhuyse et al., 2015; Hassani et al., 2018). Microbiome assembly is not a random process; rather, it is governed by a combination of deterministic and stochastic factors that operate at multiple biological levels (Nemergut et al., 2013; Zhou & Ning, 2017).

At the host level, plants actively shape their associated microbiota through a range of mechanisms, including root exudation, immune system modulation, and structural traits of tissues such as roots and leaves (Berg & Smalla, 2009; Berendsen et al., 2012). Root exudates—comprising sugars, amino acids, organic acids, and secondary metabolites—act as selective substrates that recruit specific microbial taxa from the surrounding soil (Sasse et al., 2018). Concurrently, plant immune systems function as selective filters, permitting the establishment of beneficial or neutral microbes while suppressing potential pathogens (Hacquard et al., 2017).

Beyond host-driven selection, environmental filtering plays a crucial role in microbiome assembly. Soil physicochemical properties, climate conditions, and local microbial diversity strongly influence which microorganisms are available for colonization (Fierer, 2017). This environmental dependency contributes to the high variability observed in plant microbiomes across different habitats and ecological contexts (Cordovez et al., 2019).

Transmission pathways further complicate microbiome dynamics. Vertical transmission, where microbes are inherited through seeds or vegetative propagation, can promote stability and co-evolutionary alignment between host and microbiota (Shade et al., 2012; Müller et al., 2016). In contrast, horizontal transmission from the environment introduces variability and can disrupt long-term host–microbe associations. Most plant microbiomes exhibit a mixed transmission mode, with a relatively small core microbiota maintained across generations and a larger, more dynamic fraction acquired anew (Shade & Handelsman, 2012; Toju et al., 2018).

Additionally, microbe–microbe interactions within the holobiont significantly influence community structure and function. Competitive exclusion, mutualistic cooperation, and antagonistic interactions collectively shape microbial networks, affecting both community stability and functional output (Foster et al., 2017; Coyte et al., 2015). These interactions can enhance resilience by creating redundancy and functional complementarity, but they can also introduce instability under changing environmental conditions (Mendes et al., 2011).

Understanding microbiome assembly processes is essential for determining the extent to which holobionts can be considered coherent biological units (Moran & Sloan, 2015). High variability, low transmission fidelity, and strong environmental influence may limit the applicability of holobiont-level selection, whereas stable, host-regulated microbiomes with consistent transmission patterns may support it (Douglas & Werren, 2016).

Co-Evolution, Stability, and the Unit of Selection Debate. Evidence for co-evolution within plant holobionts is clearest in specific, often binary, mutualisms and pathogenic interactions; some microbiota members show host adaptation from which mutualism can rapidly arise, and antagonistic activities that limit pathogens co-evolve within the community (Mesny et al., 2023; Rosenberg & Zilber-Rosenberg, 2018; Hassani et al., 2018; Shelake et al., 2026). Deep-time perspectives emphasize ~450 million years of plant–microbe co-evolution linked to organellogenesis, root evolution and immune "gatekeeping", generating convergent strategies in both mutualists and pathogens to modulate host immunity (Shelake et al., 2026).

Nonetheless, stable co-evolution across entire microbiomes is unlikely. Only a fraction of plant–microbe interactions are long-term and tightly integrated; many taxa are horizontally acquired and shaped primarily by environment and microbe–microbe interactions (Mesny et al., 2023; Koskella & Bergelson, 2020; Hassani et al., 2018; Trivedi et al., 2020). The notion of phylosymbiosis, where microbiomes parallel host phylogeny, suggests selection can favor host–microbiota combinations and maintain microbial cores over long timescales, but this pattern coexists with substantial individual and environmental variation (Rosenberg & Zilber-Rosenberg, 2018; Rosenberg & Zilber-Rosenberg, 2016; Hassani et al., 2018).

From a theoretical standpoint, microbiome evolution can be understood via existing multi-level selection concepts. Selection can act on hosts, individual microbes, and microbial groups, with holobionts functioning as "interactors" or "manifestors of adaptation" in some contexts (Koskella & Bergelson, 2020; Rosenberg & Zilber-Rosenberg, 2018; Roughgarden et al., 2018). Mathematical models that integrate horizontal transfer, within-host proliferation, vertical transmission and holobiont selection show that holobiont-level adaptation is possible, but depends critically on transmission fidelity and alignment of host–microbe fitness (Roughgarden et al., 2018).

Plant-microbiome evolutionary theory thus supports context-dependent holobiont selection: strong for vertically transmitted, tightly integrated symbionts, weaker where horizontal acquisition and eco-evolutionary turnover dominate (Koskella & Bergelson, 2020; Rosenberg & Zilber-Rosenberg, 2018; Hawkes et al., 2020; Hassani et al., 2018).

Microbiome-Mediated Tolerance to Abiotic Stress. Abiotic stress mitigation is a central argument for holobiont-based views of plant adaptation. Drought, salinity, heat, nutrient deficiency and heavy metals impose complex morphological, physiological and metabolic constraints on plants, including oxidative damage, osmotic stress and growth inhibition (Singh et al., 2023; Iqbal et al., 2023; Ma et al., 2020; Muhammad et al., 2024). Multiple reviews document that plant-associated microbiomes—root, rhizosphere, endosphere and phyllosphere—buffer these effects and enhance plant performance under stress (Singh et al., 2023; Ullah et al., 2025; Iqbal et al., 2023; Ma et al., 2020; Suman et al., 2022; Muhammad et al., 2024; Trivedi et al., 2020).

Mechanistically, the phyto-microbiome provides antioxidant systems, plant growth hormones, compatible solutes, bioactive compounds, detoxification of xenobiotics, sequestration of reactive oxygen species, and modulation of nutrient and water uptake (Singh et al., 2023; Ullah et al., 2025; Iqbal et al., 2023; Ma et al., 2020; Suman et al., 2022; Muhammad et al., 2024). Plant growth-promoting rhizobacteria, arbuscular mycorrhizal fungi and endophytes alter hormonal and nutrient balance, root architecture, and metabolite profiles in ways that improve tolerance to drought and heat (Singh et al., 2023; Iqbal et al., 2023; Ma et al., 2020; Suman et al., 2022). Microbial consortia, rather than single strains, frequently offer stronger and more reliable stress protection, consistent with networked interactions within the holobiont (Suman et al., 2022; Gopal & Gupta, 2016).

These microbially mediated responses can be rapid and reversible compared with plant genomic evolution, allowing holobionts to persist through environmental fluctuations while plant genomes "catch up" (Zilber-Rosenberg & Rosenberg, 2008; Rosenberg & Zilber-Rosenberg, 2016; Rosenberg & Zilber-Rosenberg, 2018). In this sense, microbiome plasticity functions as a fast-adapting component of the hologenome, potentially altering the trajectory and intensity of selection on plant stress-response genes (Zilber-Rosenberg & Rosenberg, 2008; Rosenberg & Zilber-Rosenberg, 2016; Hawkes et al., 2020; Ma et al., 2020) (Table 2, Figure 1).

Table 2

Microbiome-mediated abiotic stress tolerance in plants

Stressor	*Microbiome roles in tolerance (plant holobiont)*	*References*
Drought, heat	Hormonal modulation, improved water use, ROS control, root remodeling	Singh et al., 2023; Ullah et al., 2025; Iqbal et al., 2023; Ma et al., 2020; Suman et al., 2022; Gopal & Gupta, 2016; Trivedi et al., 2020
Salinity	Ion homeostasis, osmolyte production, antioxidant defense	Singh et al., 2023; Iqbal et al., 2023; Ma et al., 2020; Suman et al., 2022; Muhammad et al., 2024
Heavy metals	Detoxification, sequestration, altered uptake and translocation	Singh et al., 2023; Ullah et al., 2025; Ma et al., 2020; Suman et al., 2022; Muhammad et al., 2024.

This body of work supports viewing abiotic stress tolerance as an emergent holobiont property. Yet the same complexity that enables resilience complicates predictive use in breeding and biotechnology: microbiome composition is context dependent, and translating lab findings into field performance remains challenging (Singh et al., 2023; Ullah et al., 2025; Iqbal et al., 2023; Suman et al., 2022; Trivedi et al., 2020).

Applied Perspectives: Microbiome Engineering and the Future of Plant Holobiont Research. The recognition of plants as holobionts has significant implications for applied plant sciences, particularly in agriculture, biotechnology, and environmental management. One of the most promising directions emerging from this framework is the concept of *microbiome engineering*—the deliberate manipulation of plant-associated microbial communities to enhance plant performance and resilience (Afridi et al 2022).

Microbiome engineering strategies can take several forms, including the use of synthetic microbial consortia, targeted inoculation with plant growth-promoting microorganisms, and indirect approaches that modify soil conditions to favor beneficial taxa. Compared to traditional single-strain inoculants, microbial consortia often provide more robust and consistent benefits, reflecting the importance of functional diversity and synergistic interactions within microbial communities.

However, translating microbiome-based interventions from controlled laboratory conditions to field applications remains a major challenge. The context dependency of microbiome composition means that introduced microbes may fail to establish or may behave unpredictably in different environmental settings. Factors such as soil heterogeneity, climate variability, and existing microbial communities can significantly influence the success of microbiome manipulation efforts.

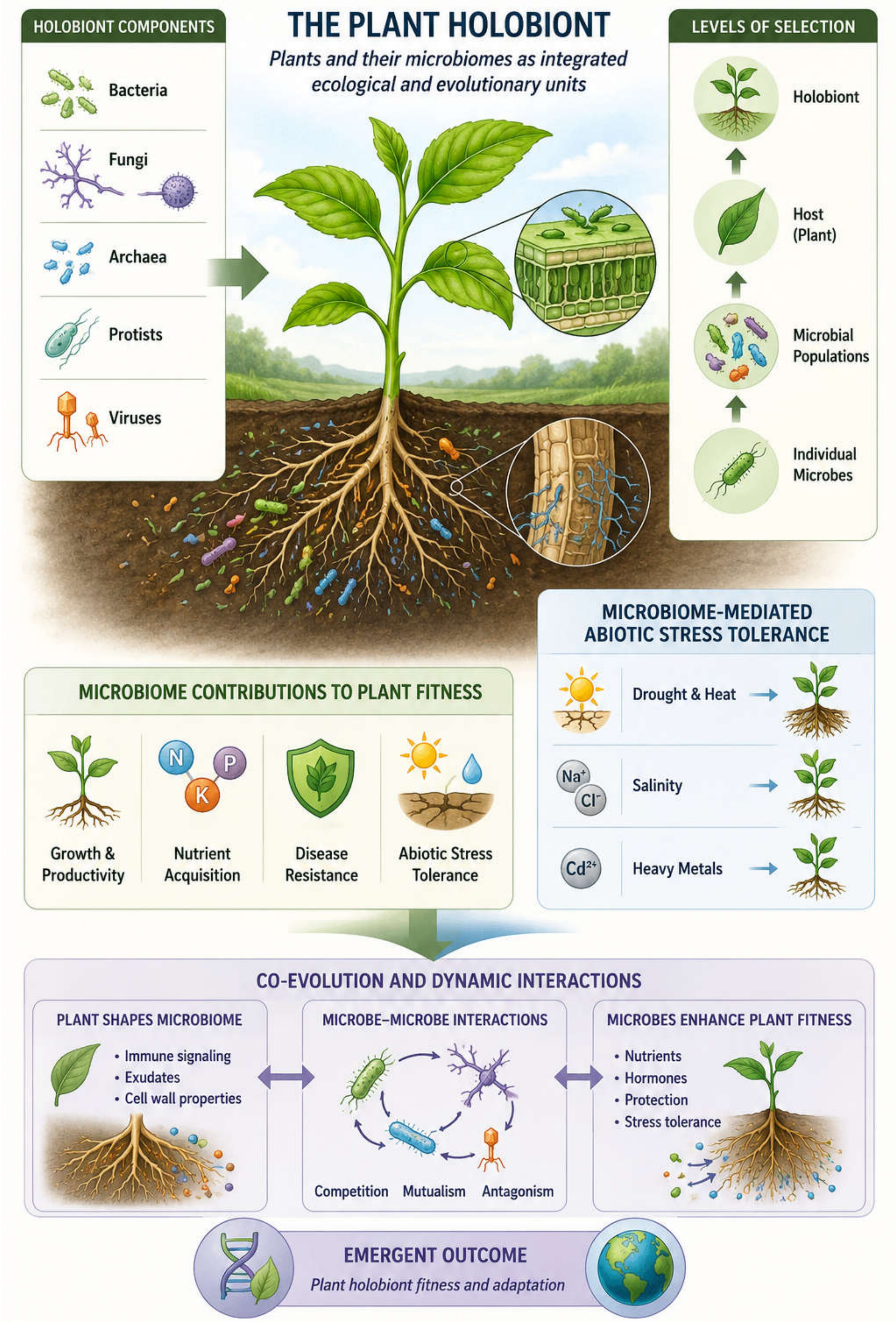

Figure 1. Representation of the plant holobiont.

Another promising avenue involves integrating microbiome considerations into plant breeding programs. Rather than selecting solely for plant genetic traits, future breeding strategies may aim to optimize plant–microbiome compatibility, promoting the recruitment and maintenance of beneficial microbial partners. This approach requires a deeper understanding of the genetic and physiological traits that govern microbiome assembly and function.

From a broader perspective, plant holobiont research also contributes to sustainability goals by offering alternative strategies for reducing reliance on chemical fertilizers and pesticides. Microbiome-mediated nutrient acquisition and disease suppression can enhance agricultural productivity while minimizing environmental impact.

Despite these opportunities, several conceptual and technical challenges remain. These include difficulties in predicting microbiome behavior, limited understanding of complex microbial interactions, and the need for standardized methodologies in microbiome research. Addressing these challenges will require interdisciplinary approaches that integrate ecology, genomics, systems biology, and mathematical modeling.

Finally, the application of the holobiont concept extends beyond theoretical debates, offering practical pathways for innovation in plant science. By harnessing the functional potential of plant-associated microbiomes, it may be possible to develop more resilient, sustainable, and adaptive agricultural systems in the face of global environmental change.

Toward a Critical Evaluation of the Holobiont in Botany. Holobiont and hologenome concepts have enriched plant biology by: highlighting the ubiquity and functional importance of microbiota; foregrounding multi-genomic contributions to plant traits; and motivating integration of ecological, evolutionary and genomic approaches (Rosenberg & Zilber-Rosenberg, 2016; Ullah et al., 2025; Vandenkoornhuyse et al., 2015; Rosenberg & Zilber-Rosenberg, 2018; Hassani et al., 2018; Gopal & Gupta, 2016; Trivedi et al., 2020). At the same time, theoretical and empirical work indicates that a full paradigm shift away from organism-centered evolution is not necessary; standard multi-level selection and co-evolutionary frameworks remain broadly adequate when carefully applied to host–microbiome systems (Koskella & Bergelson, 2020; Hawkes et al., 2020; Roughgarden et al., 2018; Hassani et al., 2018; Trivedi et al., 2020).

In botanical contexts, the most defensible position is that plants are ecological and evolutionary entities whose fitness and stress responses cannot be fully understood without their microbiomes, and that under specific conditions—strong partner fidelity, significant vertical transmission, and tight fitness alignment—the plant holobiont can approximate a unit of selection (Mesny et al., 2023; Zilber-Rosenberg & Rosenberg, 2008; Rosenberg & Zilber-Rosenberg, 2016; Vandenkoornhuyse et al., 2015; Rosenberg & Zilber-Rosenberg, 2018; Roughgarden et al., 2018; Hassani et al., 2018; Gopal & Gupta, 2016; Trivedi et al., 2020).

Conclusions. The plant holobiont concept provides a valuable integrative framework for understanding plant biology, emphasizing the essential role of microbiomes in shaping plant fitness, adaptation, and stress responses. However, critical evaluation indicates that this concept does not replace classical evolutionary paradigms, but rather complements them in a context-dependent manner. The holobiont may function as a unit of selection only under restrictive conditions characterized by high partner fidelity, substantial vertical transmission, and strong alignment of fitness between host and microbiota. In most cases, microbiome dynamics are dominated by environmental filtering and horizontal transmission, limiting the evolutionary coherence of the holobiont.

From a functional perspective, plant-associated microbiomes play a central role in nutrient acquisition, growth, defense, and abiotic stress tolerance, with these traits emerging from host–microbe interactions rather than the plant alone. Microbiome plasticity represents a rapid adaptive mechanism that can buffer environmental fluctuations and influence plant evolutionary trajectories.

From an applied standpoint, microbiome engineering and its integration into plant breeding programs offer promising avenues for the development of more sustainable and resilient agricultural systems. Nevertheless, strong context dependency and the complexity of microbial interactions remain major challenges for predictive and scalable applications.

Overall, the holobiont perspective should be regarded as a nuanced conceptual extension that highlights plant–microbiome interdependence, while remaining consistent with the robust theoretical foundations of multi-level selection and co-evolutionary theory.

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