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The Multifunctionality of the Environment in Plant Interactions: Rethinking the Concept of 'Environment' and the Extended Cognition Hypothesis

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1. *Introduction to Plant Behavior*

The purpose of this article is to explore the multiple functions that the environment can assume and perform in initiating, sustaining, and enhancing the activities of sessile (incapable of locomotion, though not of movement) and non-neural organisms (lacking a nervous system, but not complex chemical-electrical signalling systems).

To begin with, I would like to emphasize the value of situating the study of plant characteristics and behavioral strategies within a philosophical reflection (Bianchi, 2021; 2022; 2024a; 2024b; 2025).

Given their phylogenetic distance and their distinct structural, functional, and ecological organization, plants constitute a markedly different point of departure for analysis. They challenge conventional understandings of concepts such as 'behavior' (Novoplansky *et al.*, 2024), 'cognition' (Lee, 2023), 'communication' (Ninkovic, Markovic, Rensing, 2021), and 'intelligence' (Calvo & Lawrence, 2022; Khattar *et al.*, 2022). As such, they provide a valuable opportunity to refine and update distinctions in comparative studies on the set of these processes and capacities, potentially opening more integrated or alternative paths of research (Castiello, 2021).

In relation to the questions specifically examined here, plant systems could contribute to understanding what are the minimum or essential elements for attributing forms of behavior and cognition, and what is the extension of cognitive capacities and forms of communication beyond the physical boundaries of bodies in the environment, which, it should be immediately emphasized, involves the presence of other organisms (Bianchi, 2022). These considerations, in turn, contribute to a deeper understanding of the systemic and relational aspects of interspecies and interkingdom behavioral and communicative strategies (Bianchi *et al.*, 2025a).

The highly interdisciplinary nature of this research is immediately evident: the bio-ecological – and more recently, behavioral – sciences of plants are engaged in a bidirectional, multilevel dynamic through which they both influence and are, in turn, shaped and enriched by developments in a variety of disciplines. These include, in particular, cognitive science (Bianchi & Castiello, 2023a; 2023b), philosophy of mind (Maher, 2017), philosophy of biology (Yilmaz, 2021), biosemiotics and biocommunication studies (Witzany & Baluška, 2012), and also research in epistemology (Hiernaux, 2019) and process ontology (Nicholson & Dupré, 2018; Dupré, 2020).

Overall, the transversality of these analyses will help to provide a more integrated and critical view of behavioral and interactional capacities even in non-neural organisms such as plants, enriching the framework of analysis and helping to reformulate traditional issues and raise different or new questions (Bianchi, 2024b).

2. *Plants and Ecological-Relational Studies*

Ongoing research into plant abilities can expand, and in turn be integrated, by studies on systemic-relational and ecological processes that have contributed to a redefinition and gradual transformation of the very concept of environment (Gagliasso, 2013). This shift has been made possible by the development of an anti-reductionist and strongly interdisciplinary framework for the study of living systems and their interrelations, supported by a series of theoretical and scientific-technological advances aimed at addressing the multifactorial and multilevel organization of life (Bianchi *et al.*, 2025a).

Historically, the study of the complexity of reality has been shaped by the evolution and hybridization of various theoretical approaches (Hooker, 2011). Notable examples include the development of systems theories in the 1950s and 1960s, and the emergence of complexity theories in the 1980s and 1990s, which sought to account for the multiple levels of organization found in nature. These approaches have drawn to differing extents on fields such as cybernetics, information theory, and probability theory, as well as on more recent developments in the life sciences and cognitive science (Tkačik & Bialek, 2016).

For example, significant contributions have come from the work of Norbert Wiener (1948), Ludwig von Bertalanffy's *General System Theory* (1968), the study of emergent complexity in biological systems (Kauffman, 1995), and the seminal work of Maturana and Varela (1980) on the self-organization of living systems. In particular, their concept of 'autopoietic' systems refers to those capable of maintaining the cyclicity of their operational processes, between conservation and transformation, in dynamic interaction with the surrounding environment.

In the field of biological research, there has been a shift, beginning at least in the mid-twentieth century, toward increasingly relational approaches. These have progressively replaced analyses based on 'component thinking' with more systemic frameworks, in which a wide array of interacting factors and processes are considered simultaneously (Westerhoff & Palsson, 2004). In line with the research in thermodynamics and information theory (Zenil *et al.*, 2012), in molecular biology, and the rise of the so-called '-omics' sciences (e.g., genomics, proteomics, metabolomics, phenomics, etc.) in conjunction with bioinformatics, computational epigenetics, and network theory (Barabási & Oltvai, 2004), and more recently with artificial intelligence (Tahir *et al.*, 2025), new techniques, models, and software tools have been introduced. These can generate and analyze ever-increasing volumes of data to quantify and investigate the variability of biological systems within their dynamic and context-dependent relationships (Bersanelli *et al.*, 2016; Li *et al.*, 2019).

In one respect, such insights and expansions have made biology increasingly 'ecological,' given the recognition that it is not possible to study systems in isolation from their contexts of interaction. Greater attention was directed toward the environment to explain the life processes, organizational dynamics, development, and multilevel interactions of living systems. Evolutionary, developmental, and ecological processes have increasingly been understood as a set of interacting dynamics operating at multiple levels (Gilbert, 2021). This perspective is exemplified by the emergence of Eco-Evo-Devo theories (Sultan, 2007), which reflect an integrated framework that incorporates insights from several domains: ecology, which examines interactions between organisms and their environments; evolutionary biology, which investigates processes of adaptation and diversification in historically situated populations; developmental biology, which explores ontogenetic mechanisms and phenotypic plasticity, namely, the regulatory systems governing the formation and transformation of organisms during development; and the behavioral sciences, which elucidate the role of behavioral traits and responses within specific ecological contexts (Abouheif *et al.*, 2014; González-Forero, 2023).

Under a shared conceptual umbrella, living systems, regardless of the species or kingdom to which they belong, are examined in terms of their conservative and transformative interactions with the environment, characterized by recurrent and variable processes of matter recycling and energy exchange (Goyal *et al.*, 2023).

These observations pave the way for an increasingly scientifically grounded conception of the relationship between organism and environment (Corris, 2020; Milocco & Uller, 2023). Within this perspective, a plurality of dynamic interactions between internal and external factors can be identified, along the 'porous' boundaries of organisms' bodies, where a processual understanding of development becomes central (Continenza, Gagliasso, & Sterpetti, 2013). Therefore, more or less integrated perspectives emerge, depending on how narrowly or broadly one chooses to analyze the factors and processes at play within a given system, whose boundaries, in order to avoid interpretative chaos, remain functionally identifiable (Bianchi, 2024b).

2.1 *Conceptions of 'Environment'*

In this context of theoretical, scientific and technological changes, the concept of environment itself has undergone transformations, being differently characterized and consequently interpreted.

In brief, there has been an evolution of the conceptions and role of 'environment' (Moczek, 2015). For example, the perspective on the environment has evolved from viewing it as a merely external perturbing factor, incapable of significantly shaping eco-evolutionary dynamics and development, to conceiving it as a network of processes characterized by relational actions and co-constructive, co-determining behaviors (Gagliasso, 2012). Accordingly, the environment is no longer regarded simply as the 'place' of organismic life, but rather as the 'theatre' of the set of relationships and constitutive and possible processes of life. This makes us reflect, at different scales of analysis and observation of phenomena, on the relational nature of each process: things do not 'are', but 'become', 'develop' and 'influence' one another to varying degrees (Rovelli, 2014).

This approach invites a deeper ecological understanding of the concept of environment, where 'ecology' – from the Greek *oíkos* (house) and *lógos* (study) – refers to the science that examines the network of relationships between living organisms and their surroundings (Haeckel, 1866). Ecology, in this deeper sense, is to be understood as *relationship*, the science of relationship, a discipline fundamentally concerned with the web of interactions that constitute living systems and make them functionally operative (Bianchi, 2022). From this perspective, the emphasis on the *contextual* dimension in the study of life processes becomes central, ranging from the internal environment of a single cell to the global eco-system, that is, the entire biosphere (Suess, 1885; Vernadsky, 1998; Bianchi, 2021).

Approaches to the study of ecosystems have traditionally involved focusing on the analysis of numerical relationships (e.g., the number of different species present in a given environment) and functional relationships (e.g., the various roles played by organisms within trophic dynamics). Today, energy-metabolic and functional-behavioral dimensions are increasingly analyzed in an integrated manner (Jørgensen, 2012; Watt, 2013; Byrnes *et al.*, 2014; Barnes *et al.*, 2018). As with any form of research, the focus of attention depends on the research question, order and context of analysis (Bianchi, 2024b). There is no strict boundary between the 'biotic' and the 'abiotic' (Gray *et al.*, 2024); as previously noted, the environment also includes other living systems, which may coexist, cooperate, or compete within shared ecological niches.

The environment, as it relates to the analysis of life, should not be conceived as a static entity, but rather as a dynamic reality capable of performing multiple roles and functions, depending on the systems involved and their specific structural and ecological capacities (Saborido & Heras-Escribano, 2023). This gives rise to what might be described as the environment's *multifunctionality*, which emerges from the diverse interactions of organisms and underlies the origins and development of various forms of behavior and communication.

The consideration of these aspects supports the development of a view of the organism and the environment as elements in a dynamic and transformative relationship, in which changes in one can affect the other to varying degrees, despite the persistence of specific organizational structures and our epistemic awareness of the limitations inherent in a naïve model of reciprocal causality between organism and environment (Baedke, Fábregas-Tejeda, Prieto, 2021). Beyond the level of metabolic-energetic and agentive identification of systems, it remains possible, depending on the initial research question, the level and order of analysis, to delineate the (themselves variable) boundaries of the systems under investigation (Bianchi, 2024b). In any case, a more integrated and interactive understanding of the organism-environment relation, and of the variable extension of processes beyond the physical boundaries of bodies, contributes to foregrounding what may be termed the relational and extended nature of life processes and forms of communication (Bianchi *et al.*, 2025a).

3. *Ecology and Cognition: The Role of Context and Other Organisms*

In recent years, this broadening of the horizon of inquiry has increasingly influenced studies on the cognitive and behavioral capacities of organisms, at once challenging and enriching them. What is at stake is the development of a relational and process-oriented approach to the study of behavior and communication, aimed at deepening our understanding of *bio-ecological cognition* in both neural and non-neural systems (Bianchi, 2024b).

In developing an ecology of (cognitive) plant behavior, it becomes clear that the role of context and of other organisms – whether conspecifics, members of other plant species, or organisms from different kingdoms – cannot be disregarded. In this sense, the concept of a *cognitive ecosystem* or *cognitive ecology* is tied to a conception of the environment that acquires its characteristics based on specific, evolving possibilities for action and interaction (Hutchins, 2010; Mettke-Hofmann, 2014).

This analysis favors a reconfiguration of the notions of 'inside-outside' and of organismal 'independence' or complete 'self-sufficiency', not only at the physiological level but also in terms of behavior. Living systems are not solely shaped by the specific features of their lifeworld, for example, the structuring and constraining influence of gravity (Narayanan, 2023) but are also *co-inhabited* by myriads of living microsystems. They are always connected by the possibility of nourishment, reproduction and communication, to an environment, which includes the functions performed by other organisms (Gagliasso, 2013).

The development of a bio-ecological conception of cognition allows to investigate various levels of flexible behavioral capacities, related to processes of memorization, learning, anticipation and communication of information, capacities that enable organisms to adapt to changing environments and to solve problems associated with interaction and survival (Lyon *et al.*, 2021).

In summary, then, bioecological studies, alongside eco-systemic and cognitive ones, would seem to be part of a broader framework of complementary explanation of the ways of life and interaction of living systems (Bianchi, 2024b).

4. *Plants and Extended Cognition*

Within contemporary cognitive science and the philosophy of mind, some promising approaches have emerged for addressing the complex networks of interaction between living beings and their environments, and which would seem well-suited to the ongoing challenge of including plants within the landscape of behavioral and cognitive studies. Notably, in the broader context of post-cognitivism, these include the vast 4E cognition framework (embodied, embedded, enacted, and extended cognition) (Bianchi, 2021; Segundo-Ortin & Calvo, 2022), ecological psychology (Heras-Escribano & Calvo, 2019), and relational and systemic approaches (Souza, Toledo, Saraiva, 2018).

Although distinct and non-overlapping, these approaches share a common core: an emphasis on the role of the whole organism, not merely the nervous system, in relation to the environment. They emphasize environmental embeddedness, contextual relevance, sensorimotor dynamics, and perception-action coupling. Collectively, these theoretical perspectives are contributing to the development of a more inclusive and less mentalistically biased conception of cognition, potentially extended beyond the physical boundaries of the bodies, precisely in their relationship with the environment.

A study hypothesis may now be proposed to further explore the set of these interrelated elements. Within the heterogeneous research paradigm of 4E cognition, particular attention can be given to one of its theoretical strands, namely, extended cognition. In short, the central claim of extended cognition is that cognitive processes can extend beyond the physical boundaries of the body into the environment, incorporating elements that are essential for the functioning of living systems. Originally formulated by Andy Clark and David Chalmers in 1998, this idea has since generated significant debate within the fields of cognitive science and philosophy of mind (Di Francesco & Piredda, 2012).

It should be remembered that similar ideas on the extension of processes and active forms of environmental modification have also been thematized in the context of bio-ecological studies. For example, in line with the Niche Construction Theory (Odling-Smee, 2024), Japyassú and Laland (2017) observed that artificially manipulating the tension of a spider's web threads can alter its foraging behavior, prompting the spider to attend to areas of the web that were previously ignored. This suggests that spiders, like many other organisms, can extend certain behavioral and cognitive capacities beyond the physical boundaries of their bodies, embedding part of the information-processing related, in this case, to predation within their interaction with the web.

On the other hand, when referring to a form of cognition that extends beyond the boundaries of the body, one may be alluding to different possibilities, namely, that cognition is caused, facilitated, or improved by, or even constitutively dependent on, elements that lie outside the nervous system and, more broadly, the bodily systems of the organism (Bianchi, 2024b). Thus, elements external to an organism's body may play a role in causing, conditioning, or more generally enhancing the expression of its cognitive abilities, although the specific nature of this contribution varies from case to case (most examples in the literature pertain to human cognition). These various positions have sparked an intense critical debate – one that cannot be fully addressed here – concerning the potentially far-reaching implications of a radical conception of extended cognition, when excessive significance is attributed to external objects and processes (Adams & Aizawa, 2001; Rupert, 2010). Much of the critical debate can be traced back to what is known as the 'parity principle', which states that if, in the course of performing a task, an element of the environment functions in a way that, had it occurred within the brain, we would readily identify as cognitive, then, being functionally equivalent, it should likewise be considered part of the cognitive process (Clark & Chalmers, 1998; Clark, 2008). Adopting a radical vision of extended cognition could lead to extreme consequences in which it is no longer possible to distinguish between what helps the functioning of a living system and what constitutes it (Shapiro, 2021). On the other hand, one could answer that focusing on the purely functional side there would be no substantial differences between what is 'internal' and what is 'external' (but even in this case it depends on the aspects considered). According to more conservative positions (Aizawa, 2010), cognitive systems would be embedded in environments in which there are tools that facilitate, not themselves constitute the cognitive processes of living systems (Rupert, 2004).

The debate, in its various nuances (Sterelny, 2010), and in both moderate and more radical forms, remains ongoing. In any case, it can already be stated that one of the merits of these discussions is that they help us understand – based on the specific cases and contexts involved – what should be identified as the elements and processes indispensable for us to meaningfully speak of cognition, and whether, and to what extent, the boundaries of the analysis of cognition or of a given behavioral capacity should be extended. These discussions also serve to highlight the limitations of conceiving cognitive systems as 'isolated' systems (Bianchi, 2021). Certainly, a perspective that is decontextualized, non-relational, ungrounded, or based on excessively rigid criteria proves inadequate for advancing our understanding of the complexity of cognitive forms, understood as multi-process phenomena that unfold in space and time, and are shaped by both individual and intergenerational development (Bianchi *et al.*, 2025b).

For our purposes, it is noteworthy that recent work, particularly by Parise, Gagliano, and Souza (2020); Parise *et al.* (2023); Parise and Marder (2024); and Marder and Parise (2024), have explored whether the hypothesis of extended cognition can be meaningfully applied to plants. They ask whether this hypothesis is especially pertinent to plants, given their rooted nature and their continuous coexistence with other organisms within a shared growth environment.

Moreover, I would suggest that reflections on forms of extended cognition can themselves be enriched and supported by ongoing research into plant capacities. For this reason, regardless of the specific empirical outcomes, the analysis itself holds significant relevance.

4.1 *Plant Systems and Environmental Interactivity*

In this context of analysis, behavioural and communication capacities would emerge from complex interactions of signalling networks that regulate relationships over time in the exchange with the environment, which also includes other organisms (Maturana & Varela, 1980).

More specifically, in the context of extended plant cognition (EPC), the hypothesis concerns the ways in which plants extend and enhance their information-processing, sensory, behavioral, and communicative capacities beyond the physical boundaries of their bodies. This occurs through the modification of the surrounding environment, particularly via the aerial release of volatile organic compounds (VOCs), and, at the root level, through the secretion of exudates and the formation of associations with mycorrhizal fungi and certain genera of soil bacteria (e.g., nitrogen-fixing bacteria). More broadly, these processes take place through interactions with other organisms present in the environment (Parise, Gagliano & Souza, 2020; Parise *et al.*, 2023; Parise & Marder, 2024; Marder & Parise, 2024).

An example proposed to test EPC is to verify root growth after removal of root exudates, i.e. the organic compounds secreted by roots that perform signalling and modulation functions in the surrounding growth area (Parise & Marder, 2024). Thanks to the emission of root exudates, which accumulate between the exploring roots and the impediments in the soil, the plants can perceive and overcome obstacles in the soil (Falik *et al.*, 2005). Their presence can thus be interpreted as a functional extension of the plant's perceptual capacities. However, it has been observed that, beyond a certain concentration, the accumulation of these substances can become toxic to the very plant that produces them (Wu *et al.*, 2007; Asaduzzaman & Asao, 2012). One hypothesis to explain this result is that exudates help plants distribute their roots in the soil more effectively (Semchenko *et al.* 2008; Caffaro *et al.*, 2011). After the removal of the exudates, the roots grew towards obstacles, for example nylon ropes in the case of the experiment by Falik *et al.* (2005), as if they were not there (Parise & Marder, 2024).

This aspect contributes to strengthening the hypothesis that plants, despite having, like any other biological system, their own biological signalling networks and their own internal processes of organizing, transmitting and storing information (Trewavas, 2004), rely significantly on external modes of perception to detect environmental elements and obstacles around their growth area.

Furthermore, plants, as sessile organisms, are closely rooted to their living contexts: many physiological processes and plant behavioral activities can occur because plants interact with members of their own species, other plant species and, above all, with an exorbitant number of organisms of microbial communities. On a general level, it should be remembered that the assembly of the plant microbiome is a complex ecological process driven by processes of interaction and coevolution over the long range (Dini-Andreote & Raaijmakers, 2018; Trivedi *et al.*, 2020).

At the inter-organism level, the different bio-ecological interaction that plants can have are commonly referred to as 'symbiosis'. We know that in the natural world there are diverse types of symbiosis (mutualism, commensalism, parasitism), where some of these relationships are beneficial for both organisms involved, others beneficial only for one and indifferent for the other, still others beneficial for one and harmful for the other (Oubohssaine, Rabeh, Hnini, 2025). On the other hand, these are not static categories, and different forms of symbiosis may shift into one another as environmental conditions and community composition change.

I now briefly recall some of the benefits that plants derive from their interactions with the microbiota (composed of bacteria, fungi, protozoa and viruses).

With regard to bacterial communities, it is well established that certain plants associate with bacteria such as those of the genus *Rhizobium*, which can convert atmospheric nitrogen into forms accessible to plants (Granada *et al.*, 2023). Furthermore, studies have demonstrated that plant roots, such as those of *Arabidopsis thaliana*, engage with bacterial communities through specific biosynthetic pathways that produce compounds capable of shaping and modulating distinct microbial assemblages in the rhizosphere (Huang *et al.*, 2019). These microbial communities, depending on their composition, can encode 'chemical memories' of the soil, thereby influencing the plant's subsequent development and fitness. The information stored via the root-associated microbiota thus constitutes a form of 'soil legacy' (Hannula *et al.*, 2021). It has been suggested that the altered microscopic community forms a kind of physical representation of a past event stored outside the plant's body, the significance of which only emerges when the plant interacts with it. In this case, what may be described as a form of ecological memory, instead of being conceived as an exclusively internal storage system, is located between the plant and its underground environment, forming a coupled system, capable of conditioning the subsequent development of the plant and the microbial community (Parise & Marder, 2024). In this sense, it could be said that the perceptual-agentive and information recognition processes, relating to the soil legacy, constitute an exchange of interkingdom processes, involving phylogenetically diverse organisms (Bianchi, 2024b).

In summary, the modulation of the chemical composition of root exudates is an active process partly controlled by the plant, capable of altering the microbiota, and consequently of modulating the impact of environmental stressors on plant fitness (Bai *et al.*, 2022). These interactions leave organic traces in the environment that help shape present conditions and guide future interactions (Hu *et al.*, 2018).

Regarding mycorrhizae – symbiotic associations between the roots of many plant species and fungi – it is well established that the fungal partners, lacking the ability to perform photosynthesis, receive sugars and other organic compounds from the host plant. In return, they supply water and mineral nutrients, particularly phosphorus and nitrogen, thereby enhancing the plant's nutrient uptake efficiency (Wu *et al.*, 2024). The structural flexibility of fungal hyphae, composed of chitin-rich cell walls (as opposed to cellulose in plants), enables them to grow across long distances in the soil and to overcome physical barriers, facilitating nutrient foraging. Additional advantages arise from their much smaller size, which allows them to explore soil pores inaccessible to roots and root hairs, while requiring less carbon investment per unit of soil explored; furthermore, they grow faster than roots and possess enzymes absent in plants, enabling more efficient mobilization of soil nutrients. Mycorrhizal associations support plants in detecting and acquiring nutrients and water, and in mitigating the effects of distant environmental stressors. Acting as both biofertilizers and bioprotectors, they enhance the plant's capacity for perceptual processes and signal reception (Ferlian *et al.*, 2018; Begum *et al.*, 2019).

When asking what the EPC hypothesis contributes to the processes studied in plant physiology, one could argue that, from an ecological-behavioral perspective, microorganisms and mycorrhizal fungi located outside the plant body play a crucial role in enabling the effective expression and potential enhancement of plant responses to environmental challenges. In summary, these types of associations can improve the plant's overall capacities for perception, memory, and signal transmission of environmental information in response to various stimuli and stressors. These cases are particularly relevant because they involve processes of communication, self- and non-self-recognition, and forms of cooperation and competition shared among organisms belonging to different species and kingdoms (Parise, Gagliano, Souza, 2020; Bianchi, 2022).

4.2 *The Meanings of 'Extended' in Cognition*

At the level of theoretical reflection on extended cognition, Parise and Marder (2024) have indicated three main meanings of *extended*. The first meaning refers to extension beyond the mind: in this case, as a surface, in contrast to the Cartesian conception, according to which the thinking thing (*res cogitans*) was, in fact, non-extended, that is, it did not possess an existence grounded in space, unlike the material nature of the extended thing (*res extensa*) (Descartes, 1641). It should be noted that even when remaining at the level of brain function, on a microscopic scale, the brain is extended and occupies space, albeit confined to the skull (Marder & Parise, 2024). The second meaning is extended beyond cognitivism, with the aim of overcoming the epistemological-interpretative limits of the modern notion of cognition (or of a certain conception of the mind). The third meaning of extended highlighted by the authors, specifically with reference to plants, refers to the extension of abilities into the environment, beyond the physical boundaries of plant bodies. This perspective emphasizes that these living systems operate as expanded networks of possibilities for initiating and sustaining processes of communication and survival. In this sense, by reiterating the non-absolute autonomy of plants, they are understood as nodes within a functionally extended network, challenging the notion of rigid boundaries and promoting a view centered on the dynamic flow of activity across multiple levels.

Compared to the idea that cognition involves the processing of information, even in plants, as in any living system, there are networks of signalling and non-random organization of information (Bianchi & Castiello, 2023a), despite the fact that the conventional division between internal and external in these organisms is even more nuanced, with greater emphasis given to the relationship with the external context of life.

As Parise and Marder (2024) note, while animals possess internal organs, most plant organs are in direct contact with the external environment: plant life, in general, occurs more at the surface. Plants with an open body plan actively extend their perceptual and behavioral capacities through the growth of tissues and organs. These capacities expand alongside the physical expansion of the plant body, with continuous growth generating new possibilities for environmental interaction (Marder & Parise, 2024). For instance, the surfaces of plant organs, such as leaves and roots, serve as interfaces with the external environment, which itself comprises other living systems and elements. This suggests that, in terms of environmental dependence, plants are deeply integrated into their surroundings. They live in close continuity with their growth substrate, and the behavior of the whole plant emerges from the temporally distributed functions of distinct modules, each interacting with its local environment (Lüttge, 2019). While animals express many aspects of their behavior through movement, understood as self-locomotion or self-displacement, plants – despite also exhibiting forms of movement (Bianchi *et al.*, 2025a; 2025b) – respond to external challenges through phenotypic plasticity. This often involves growth and a series of changes that can alter their interactions with the surroundings (Marder & Parise, 2024).

4.3 *Further Implications of the EPC Hypothesis: Challenging the Concept of the Individual Agent*

A deeper understanding of the distinctive characteristics and modes of life and interaction in plants can contribute to enriching our conceptions of extended cognition, and more broadly, our understanding of the levels and forms of agency and natural cognition.

For example, one might ask who (if any) is the 'cognizer,' that is, whether there exists, in plants, an organization at the level of the whole organism that perceives and behaves in a coherent, integrated manner: pursuing survival goals, recognizing features and elements of its surroundings, and distinguishing between what is beneficial and what is harmful or should be avoided (Marder & Parise, 2024; Bianchi, 2024a). Indeed, it has been repeatedly argued that, in plants – as non-neural and modular organisms, and thus divisible – it is not appropriate to speak of true *individuality*. A plant can be dissected or lose a substantial portion of its biomass without dying, although this resilience varies considerably across species (Mancuso & Viola, 2013). According to this view, the lack of effective information integration at the level of the whole organism would preclude plants from producing coordinated and relatively unified responses directed toward survival goals (Firn, 2004). In summary, plant modularity lies at the core of the debate concerning their purported lack of individual behavioral capacity. However, some authors have challenged this view (Trewavas, 2004), arguing that plants must develop all essential organs for survival, possess both locally integrated and systemic signalling mechanisms, and are indeed capable of responding in a relatively coordinated and ecologically targeted manner, based on their specific environmental demands (Segundo-Ortin & Calvo, 2023). Therefore, even if neural and non-neural organisms are systems with different levels of speed of information integration, the fact remains that each system has a non-random organization of information, at least functional to carry out essential signalling and survival activities (an aspect already visible from cellular organization), so as to maintain agent-functional coherence for the entire life span of the organism (Bianchi & Castiello, 2023a;

McMillen & Levin, 2024). This is a non-trivial point. It is worth noting, for example, that the lifespan of certain plant organisms, particularly trees, can range from several decades to over a thousand years. Such an achievement can hardly be attributed to mere chance at the level of information organization and transmission.

In light of the extended cognition hypothesis, we are prompted to revisit, through a renewed perspective, the question of what constitutes the basic and emergent units involved in behavior, communication, and interaction within an environment (Bianchi, 2021).

Parise and Marder (2024) distinguished several meanings of the EPC hypothesis. Among these, for example, a 'strong' interpretation posits that the minimal unit is composed of the plant together with its environment, specifically, the elements of its immediate surroundings, both above and below ground, such that it is meaningless to consider them separately. A 'weak' sense maintains that the plant constitutes the primary unit, with its interactions with the environment regarded as secondary or additional, albeit essential for achieving a comprehensive framework of analysis.

A further implication of this analysis, closely related to the above, concerns the challenge that *plant difference* poses to the traditional concept of the 'individual' (Bianchi, 2024b), a challenge that is particularly salient in the case of plants (Yılmaz & Dupré, 2025).

At a more fundamental level, within the context of biological research, when we ask how 'individuality' should be understood, we find that it has been defined in multiple ways. For instance, it has been investigated in relation to genomic uniformity, though not without important nuances and exceptions (Baluška & Mancuso, 2021). In plants, for example, the widespread phenomenon of genetic mosaicism complicates this notion (Tomimoto & Satake, 2023). Moreover, it is well established that organisms, even when sharing the same DNA, host numerous endosymbionts; in humans, for instance, bacterial cells outnumber human cells. As such, it may be more accurate to conceive of organisms as 'shared' or 'co-inhabited' systems, engaged in continuous interaction with myriads of other biological entities (Gagliasso, 2019).

A concept that is increasingly used today to describe these multifactorial processes of multi-individuality is that of the *holobiont*. The term 'holobiont', advanced in particular by Lynn Margulis beginning in 1991, refers to the biological unit composed of a host organism and its symbionts. Strictly speaking, the eukaryotic cell, together with its symbiotic organelles, constitutes a cellular holobiont. The concept was later expanded to encompass multicellular hosts with significant endo- and exosymbiotic associations (Baluška & Reber, 2021).

Moving the analysis to the macroscopic and even supra-organismic level, emergent properties arise from the multilevel interactions among various elements and processes, as seen, for example, in the signalling and resistance capacities to environmental stressors observed in forests, which exceed those of any single plant (which is, in any case, never truly isolated). At this point, we are reasoning at an ecological-relational level (Gorzelak *et al.*, 2015). Even if only for practical reasons, when we ask where to place the boundary, the answer depends on us, on where we direct our attention, what our initial question is, and the level of analysis applied to the system under consideration (Bianchi, 2024b).

If, in the case of plants, one cannot speak of 'subjectivity' – and, according to some, even 'individuality' becomes a problematic notion, albeit with due exceptions (Baluška & Mancuso, 2021) – should we then abandon the concept of the 'individual' altogether? (Bianchi, 2024b). Rather than referring to plants as 'pre-individuals', a term that points to an ongoing process of individuation, retaining an unstructured, potential dimension yet to be specified (Faucher, 2014), but which risks being misinterpreted as implying a deficiency or lack relative to the animal paradigm (Baker, 2017), we might instead reason in terms of an individual 'history' or 'life path,' unique and specific to each living being. This would reflect an initial constitution shaped by the series of interactions experienced by individual plants throughout their development within specific environments, interactions that lead them to express certain traits more strongly and to respond in distinct ways to various environmental challenges (Bianchi, 2024b).

Every living system, including plants, therefore presents an individual life path, distinguishable at the metabolic-energetic and functional-agentive level, which allows the system both to behave while preserving its organization in space and time and to plastically modify its phenotype. Even in what seems to be an oxymoronic expression, vegetal 'modular-individuality' (Bianchi, 2024b), there is some organization of environmental information and coordination of physiological and behavioral processes at various scales, based on specific ecological needs (Yilmaz & Dupré, 2025).

5. *Conclusion*

In line with the ongoing debate on the role and systemic reach of bio-ecological cognition (Huebner & Schulkin, 2022), these considerations on the hypothesis of extended cognition in plants provide an opportunity to further explore, within the fields of cognitive science, philosophy of mind, and comparative behavioral studies, which systems and processes are involved in forms of cognition and what is the extension of behaviors that can be meaningfully interpreted as cognitive beyond the physical boundaries of bodies.

The ever-present question is where (how and why) to place the boundary (Bateson, 1972).

Recognizing the complexity of reality and the plurality of our epistemological efforts to understand it (Hooker, 2011), there is a growing tendency to argue that no living being – plants in particular, due to their deeply rooted nature and the cooperative/competitive coexistence with their neighbors – can be considered in isolation from its relationships with other organisms, despite the system's inherent properties of uniqueness and self-organization. A conception of the environment as interactive and dynamic, which includes the strategies of other organisms, can undoubtedly contribute to a deeper understanding of various forms of communication and cognition (Bianchi, 2024b).

Among the most compelling aspects of this conception of the environment are its implications for the study of communication forms that aim to detect ecological properties potentially endowed with a 'transversal' value, that is, signals that are chemically 'understandable' by very different organisms. Despite differences in structure, organization, and ecology, there appears to be a shared ground in which the signals are 'recognizable' and effective in eliciting targeted responses appropriate to the context of interaction (Bianchi *et al.*, 2025a). The interplay between internal and external pathways of interaction and communication reshapes our understanding of communication itself, revealing it as a far more complex, interspecific, and even interkingdom process, that involves not only organisms of different species but also those belonging to different biological kingdoms.

This body of research on the nature and extent of interaction and communication processes among living beings contributes to the development of an ecological and process-oriented conception of cognition, one that approaches plant activity and cognitive behavior as a set of processes that are partly conserved and partly variable over time. These processes evolve both throughout the organism's lifespan and in relation to what is transmitted to future generations, as well as through the conditioning traces left in the environment, which can influence various intra- and interspecific forms of interaction (Bianchi, 2021; 2024b). A purpose will therefore be to improve the study of forms of behavior and communication, considering their extension in the environment and the temporality of the processes (Kiverstein & Sims, 2021; Bianchi *et al.*, 2025b).

The environment contributes to shaping an organism as the particular being it is and conditions, though does not determine, what it will become over the course of its individual development. In the case of plants, this is visibly expressed even in their differently branched structures (Bianchi, 2022).

An attempt will be made to better understand how, in the case of plant, and in the case of other non-neural organisms, the context and the 'others', the presence of other organisms, affect the possibility, development and transformation of signalling and behavioral capacities.

These considerations are not only of theoretical relevance but may also have practical consequences.

The EPC hypothesis can contribute to the development of more refined agricultural practices by enhancing the management of external factors affecting plant life. This includes careful selection of both plant and non-plant species in the surrounding environment, an approach particularly relevant in the current context of climate change and global warming, which are capable of altering microbial communities and influencing plant responses to microorganisms and pathogens (Mukhtar *et al.*, 2023; Kaur *et al.*, 2025).

Finally, in light of these ecosystem interactions that involve us in a world shared with other species, it is worth recalling Bateson's insight in *Steps to an*

Ecology of Mind (1972): the unit of survival is the organism plus the environment. Given the profound anthropogenic impact on ecosystems, we are increasingly learning that an organism which destroys its environment ultimately destroys itself, since the environment, as has clearly emerged, is not a passive external backdrop or container but a constitutive and interactive element (Bianchi, 2021). Without dissolving boundaries, it can be said that organisms are to a large extent shaped by what surrounds them, beginning with what they feed on and are, in turn, composed of.

Given the dense network of intertwined processes, increasing attention is being devoted to a view of the environment as a common good that must be proactively safeguarded in order to address the consequences of short-sighted actions on processes unfolding across widely varying spatial and temporal scales. These very processes contribute to shaping us and will determine the conditions for our future well-being and survival.

And in this unfolding phase of transformation, we still have much to learn from plants.

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– The Multifunctionality of the Environment in Plant Interactions: Rethinking the Concept of 'Environment' and the Extended Cognition Hypothesis

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ABSTRACT
This paper explores connections between studies on plant interactive abilities and (1) systemic-relational and ecological approaches, and (2) the framework of extended cognition. The first connection focuses on the transformation of the concept of environment – from a backdrop for organismic life to a constitutive and formative element of the 'agent-environment' system – arising from systems theory in dialogue with ecological studies and epistemological approaches to complexity. The second connection examines the post-cognitivist theoretical approach of extended cognition, which can offer valuable insights into how research on plant capacities might be oriented, particularly regarding the role of the context and the presence of other organisms. The interconnection between these levels lays the groundwork for future investigations not only into plant abilities, but also into philosophical approaches aimed at developing a conception of cognition as a historically, relational, and context-dependent process that can be functionally extended beyond the physical boundaries of individual organisms.

KEYWORDS
Environment; Plant Extended Cognition; Multifunctionality

SOMMARIO
La multifunzionalità dell'ambiente nelle interazioni tra piante: ripensare il concetto di "ambiente" e l'ipotesi della cognizione estesa. Questo articolo esplora connessioni tra gli studi sulle capacità interattive delle piante e (1) gli approcci sistemico-relazionali ed ecologici, e (2) il quadro della cognizione estesa. La prima connessione si concentra sulla trasformazione del concetto di ambiente – da sfondo per la vita degli organismi a elemento costitutivo e formativo del sistema 'agente-ambiente' – derivante dalla teoria dei sistemi in dialogo con gli studi ecologici e gli approcci epistemologici alla complessità. La seconda connessione esamina l'approccio post-cognitivista della cognizione estesa, che può offrire preziose intuizioni su come potrebbe essere orientata la ricerca sulle capacità delle piante, in particolare per quanto riguarda il ruolo del contesto e la presenza di altri organismi. La interconnessione tra questi livelli getta le basi per future indagini non solo sulle capacità delle piante, ma anche su approcci filosofici volti a sviluppare una concezione della cognizione come processo storico, relazionale e dipendente dal contesto che può essere esteso funzionalmente oltre i confini fisici dei singoli organismi.

PAROLE CHIAVE
Ambiente; Cognizione estesa nelle piante; Multifunzionalità