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# Extended plant cognition: a critical consideration of the concept

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**Abstract** Within the framework of studies of plants as cognitive organisms, there is a hypothesis that plant cognitive processes are not enclosed within their bodies but extend to the environment. The extended plant cognition (EPC) hypothesis suggests that when plants modify the environment around them through the release of volatile organic compounds (VOCs), root exudates, and the sustenance of mycorrhizal networks, they extend their sensorial apparatus and externalize a part of their information-processing system. As a result, a plant can no longer be seen as an isolated organism easily distinguishable from its milieu. In this article, we discuss the implications of understanding plants as extended cognitive organisms and assess four test cases that corroborate the EPC hypothesis, one for each possible channel of extended plant cognition discussed here. We conclude that this new approach can redefine how we understand plants and their environment. EPC may also be a fruitful source of inspiration to develop new techniques in agriculture by enhancing the external elements of plant cognition.

**Keywords** Root microbiota · Soil-borne legacy · Mycorrhizal networks · Mycorrhizas · VOCs · Root exudates · Plant ecophysiology · Plant ecology

## 1 From internal to extended cognition

Proposing an information-processing model for thinking and problem-solving, cognitivism identifies the Central Nervous System (CNS) and, in particular, the brain, as the locus of cognitive activity. However, the psychological notion of cognition has a long prehistory in philosophical approaches to the concept of thinking. For Plato and Aristotle, the seat of the "rational soul" is the head. The former philosopher considers the brain to be a link between the human body and the celestial realm of Ideas (Plato 1929, p. 90a–b); the latter distinguishes the rational from the nutritive (shared with plants) and the sensitive (shared with animals) kinds of soul, or principle of vitality, even though he maintains that the thinking mind (*nous*) is not "mixed with the body" and has "no actual existence until it thinks" (Aristotle 1975, p. 429a).

At the dawn of European modernity, Descartes equates the existence of the thinking mind with one's existence *as such*, resulting in his dictum "*Cogito,*

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*ergo sum*" (I think, therefore, I am; *Je pense, donc je suis*), raised to the status of the first principle of his philosophy (Descartes 1874). Descartes dispenses with the idea of the ensoulment of non-human living beings, notably of plants and animals, which is prevalent in pre-modern philosophical tradition. The human being, in turn, becomes the cognitive being par excellence, one whose very existence is defined by, and logically derivable from, cognition. Consequently, the mind/body problem, already palpable in Aristotle, becomes further accentuated (and, in the second half of the twentieth century, is reproduced in the therapeutic split in clinical psychology between psychanalysts and behaviorists). Likewise, Descartes follows Plato and Aristotle in their insistence on the uniquely human capacity to think, denying it to other living beings. This means that sensation, nourishment, and reproduction in other animals and plants happen without discernment, decision-making processes, and other interventions of thinking.

The dualism of the mind versus the body started to be challenged in the 1970s, when many researchers questioned the CNS as the sole locus of cognition. Scholars began to develop the thesis that the mind is not a thing (*res*), something that *is* in the head, but rather a process that *happens* in living bodies. What we understand by mind, or cognition, is the result of a very complex interaction between the elements that constitute the living body, where these continuously adjust their relations through time and in an ongoing exchange with the environment (Bateson 1972; Maturana and Varela 1980).

Whereas the brain is important for the proper cognitive functioning of the organisms that evolved brains, cognition is not entirely restricted to it, but emerges from the interaction of all organs beyond the brain—especially those responsible for sensing and moving—with the environment. This special, adaptive interaction of the living organism with the environment allows it to improvise when external conditions suddenly change, or to forecast future conditions, ensuring that the system is not disrupted by environmental fluctuations, and, therefore, to a great extent, guaranteeing survivability. On this view, cognition would be a definitive characteristic of life, and life without cognition would be impossible. It is a process present already in our last common ancestor, the process that was important to keep it alive and reproducing, and that evolved with every branch in the tree of life. The more sophisticated the sensorial apparatus of organisms, the more possibilities for engaging with the environment were created, and the more room was available for complex forms of cognitions to emerge, ultimately resulting in the diversity of life forms and cognitions we have today (Maturana and Varela 1980; Lyon et al. 2021).

Since cognition is a property of living bodies, and their life is only possible because of the tight interaction of the sensorial apparatus of organisms with the environment, it is said that cognition is *embodied* and *embedded* (Newer et al. 2018). Furthermore, since cognition is a process, it expresses itself through "perceptually guided actions" in the world, meaning that cognition is *enacted* too (Varela et al. 2016). Varela et al. (2016) put much emphasis on movement and sensorimotor capacities, but of course this is not entirely applicable to plants. Many plant actions happen at the metabolic level, like adjustments of photosynthetic rates and the exudation of chemical components. As it may be clear at this point, however, the environment has a critical role in cognition, for it is only through a dynamic interaction of the cognizing system with the environment that the emergence of cognition is possible.

Clark and Chalmers (1998) proposed taking a step further in the assessment of the role of the environment in cognition. They suggested a form of externalism where the human mind would not be confined to the skull and the body and would extend to objects in the environment when they are manipulated by the cognitive agent. In a classical example, an individual writing the address of a museum in a notebook and using it to remember how to get to the museum would be externalizing part of their memory outside their brain, and the notebook with information would be part of the individual's extended cognition.

The idea that human cognitive processes partially happen outside the body is very controversial, and it has been debated in the philosophy of mind ever since. Some argue that to be considered cognitive, the object must present a "mark of the cognitive" (Adams and Aizawa 2001), but such an unequivocal mark was never found. Others argue that the mere fact that we manipulate objects to aid our cognitive process do not mean that they are part of our cognitive process (Gallagher 2018), and criteria for delimiting the boundaries of cognition have been proposed (Adams and Aizawa 2001; Kaplan

2012). It is not within the scope of the current paper to delve into this discussion, but a compilation of essays debating the extended cognition hypothesis in humans can be found in Menary (2010). Some recent empirical evidence for human extended cognition includes Bocanegra et al. (2019), Armitage et al. (2020), Armitage and Redshaw (2022), and reviewed in Gilbert et al. (2022).

The explanatory power of extended cognition was not restricted to humans, but applied to explain the complex behavior of non-human primates (Mosley and Haslam 2016; Mosley 2021) and spiders (Japyassú and Laland 2017), whose webs would consist of part of their perceptive and information-processing apparatus, without which their cognitive process is significantly reduced. Even non-neural organisms like slime molds (Sims and Kiverstein 2021) and plants (Parise et al. 2020, 2023) were proposed as extending their cognition. Besides, according to Parise et al. (2023), it is possible that the phenomenon of using the environment to extend cognitive process is much more common than usually thought, potentially being present in organisms as diverse as protists, termites, mice, and even tumorous cells.

A shift from internal to extended cognition has important implications for how we understand human thinking, as much as for a broader reassessment of the cognitive capacities inherent to non-human organisms. With thinking decentered from the brain and the CNS, perception and sensation are integrated with the more abstract capacities of the mind. The peripheral nervous system (PNS) is no longer analytically separated from CNS—as it is also not anatomically or physiologically—and the mind/body split becomes obsolete. It's known, for example, that the movements of skeletal muscles are important to the modulation of our thinking (Dutriaux and Gyselinck 2016; Johansson and Johansson 2014; Onishi et al. 2022) and even of our emotions (Coles et al. 2019). The tight connection of the gut microbiota through the gut-brain axis has been revealed to be prominently active in the cognition of humans and rodents (Carlson et al. 2018; Chevalier et al. 2020), which are model organisms for studies of mammalian cognition. In turn, animal perception and sensation are no longer regarded either as qualitatively distinct from or as inferior to the human variety; the sensory-perceptive apparatus, too, is part of extended cognition, including its medium and objects organized in noetic-noematic correlations (Husserl 1983; Merleau-Ponty 1964).

What specifically interests us in the current article, however, is extended cognition in plants. Plants also sense and perceive fluctuations in their environments, registering several kinds of environmental cues and multiple interactions among these simultaneously (Trevawas 2003, 2004, 2005; Karban 2015). Our point is that these are not merely phenomena of sensation and perception, of signaling and communication, but that they could constitute part of extended plant cognition (EPC), which is, in fact, not only extended but also dynamically extending in growth. How this kind of cognition works and what it implies with respect to cognition more generally understood are some of the questions we want to raise anew here.

## 2 Three senses of 'the extended' in plant cognition

Before proceeding, we suggest three interpretations of the qualifier "extended" in "extended cognition." The first two are applicable to all types of extended cognition; the last is unique to plants and forms the starting point for our reflection.

### 2.1 First sense: extended as of or on the surface; space-based

The attribution of extension to cognition is overtly anti-Cartesian. For Descartes, the thinking thing, *res cogitans*, was, precisely, non-extended (had no spatially-based existence), in contrast to the materiality of the extended thing, *res extensa* (Descartes 1874). The attribution of extensionality to the cognition overcomes the mind/body split, renders cognitive processes and structures material, and also imparts to them the attributes of space (notably, external existence and divisibility), which Descartes adamantly denied as having any bearing on the mind. This means, besides the mind's finitude shared with material existence, the inevitable dispersion of cognitive processes, the divisibility of attention, and the unavoidability of distraction (Marder 2011). It also means that in parallel to the physical or metaphysical depth, in which thinking (or information processing) would take place as in a black box of sort, it is the surfaces and the interfaces of living bodies that are the sites of thinking.

### 2.2 Second sense: extended as going beyond the epistemological limits of the modern notion of cognition and of cognitivism

There are hints as to this interpretation in our elaboration on the first sense of 'extended' thinking, which scrambles the rigid distinctions between *res cogitans* and *res extensa* in Descartes. Although from a post-Cartesian perspective, this epistemological transgression seems outlandish, it is in sync with the ancient notion of the embodied soul (a principle of vitality suitable to each type of organism). For instance, one of Aristotle's definitions of the soul is "the first actuality of a natural body with organs [*entelecheia hē prōtē sōmatos phusikou organikou*]" (Aristotle 1975, p. 412b). Similarly, Plotinian insights into "contemplation of the One," which is interior theorizing or abstract thinking only in the case of human beings, resonate with cognition outside the modern stricture (Plotinus 1966, III.8.1, 1–8). Extended cognition recovers in a different way an ancient approach to thinking commensurate with extension.

### 2.3 Third sense: extended *plant* cognition as the extension of cognitive processes beyond the physical limits of a plant

This third sense of the term is, perhaps, the most counterintuitive and one that we hope to elucidate, while hinting at its potential to inform the theoretical and empirical studies of extended cognition as such. Here, not only the surfaces of plant organs (leaves and flowers, roots and stems, as well as, crucially, meristems) but also the interfaces between these surfaces, the environment and other forms of life (fungal, bacterial, insect, and so forth) function as a dispersed network of cognition. It follows that extended plant cognition is not exclusively situated in plants as its autonomous subjects; rather, plants are the nodes in the field of extended cognition, which exceeds their embodied limits.

## 3 Plants as cognitive subjects: lessons from vegetal anatomy and physiology

According to Maturana and Varela's theory of autopoiesis (Maturana and Varela 1980), a critical characteristic of living bodies is that they are defined by the dynamic of the body itself, and this is what distinguishes them from the environment as a system. If we study the world as a network of interactions, we would observe that there are certain clusters of processes and elements interacting more among themselves (there are more links between their elements) than with other processes. Within these clusters, the dynamic generates new elements, which replace decaying ones, and also set the boundaries between the cluster and other elements in the network (Di Paolo and Thompson 2014). In other words, these clusters present operational closure, and such systems are what we call living organisms.

Operational closure is how the dynamic of a system defines the system as such, distinguished from the environment (Maturana and Varela 1980; Di Paolo and Thompson 2014). Many of the links between the elements of such systems are channels of communication that allow the integration and maintenance of the system. At the same time, there are links with environmental variables that influence the internal dynamics of the system by altering its internal structure (Souza et al. 2009). It is conceivable that the more links between the elements of the system and the environment, the more possibilities of the system influencing the environment or being influenced by it.

If we analyze plants and animals from this perspective, we will notice some fundamental differences between the organization of these systems, with implications for how their modes of cognition work. The differences between plant and animal cognition arise from the body organization and evolutionary history of both lineages. As mentioned before, through the course of evolution, the different sensorial apparatuses, evolutionary history and specific needs led to the development of very different cognitive systems. To begin with, we interpret animal cognition as oriented primarily *inwards*, while plant cognition is oriented primarily *outwards*, in keeping with their respective anatomies, physiologies, or organization. For its part, this critical difference in orientation changes the operations of perception and/as action.

Because plants are autotrophic, the first multicellular photosynthetic organisms did not need to move to harvest the energy and matter they required to survive. Solar energy is abundant and fairly constant, and small molecules and nutrients would come passively to early algae and plants through diffusion in the air or water. This led to a sessile lifestyle.[1] For their part, most animals are heterotrophic. The first Eumetazoa animals had to move to find food once they depleted the nutrients of one area. This contributed to the evolution of a mobile lifestyle.[2] The different lifestyle of plants and animals led to the evolution of distinct anatomies, perceptual apparatuses, ways of relating with the environment, and consequently, different cognitions.

A typical animal can be seen as a pack of organs that can be moved around when necessary. Therefore, it needs to be as ’compact’ as possible, with implications for how its body organization evolved: centralized organs, a relatively centralized cognition, etc. Animals face issues like thermal regulation, and their centralization of functions also helps with this, for they tend to present low surface/volume ratios. Additionally, animals present relatively few senses, and these are generally centralized, too: eyes are for sight, tongue for taste, nose for smell, vestibular system for balance, and so forth. There is a remarkable exception which is the surface (skin or other similar organs) and everything it can sense, like touch, temperature, and electrical fields in some animals. But even in these cases, most of the nervous terminations will be located in the extremities. When an animal perceives something through these senses, like the smell of food, it will bring its organs towards the positive stimulus and distance itself from the negative one (or from the absence of stimuli), and having the relevant organs tightly packed helps the task (Fig. 1).

By contrast, the sessile and autotrophic mode of being of plants means that, for them, it is optimal to have the highest exposure possible, and they maximize exposure by having an immense surface area. Think of all the leaves of a tree gathering sunlight, or all the roots looking for minerals and water in the soil. While some animal organs are never in direct contact with the external environment, virtually all plant organs are in tight connection with it. This is why there is value in talking about “internal organs” in animals, a concept that has no sense if applied to plants. In sum, plants are outward-oriented because their life happens on the surface. Besides, plants are modular. They do not have (and never could afford) centralized organs. Their vital functions are scattered throughout the entire plant, and every module is semi-independent, able to solve problems and interact with the environment locally, regardless of its capacity for communication with others (Peak et al. 2004; Matthews et al. 2017; Lüttge 2019) (Fig. 2).

The life of a plant transpires on the surface, inviting the closest interaction with the environment, more so than it does in animals—and this superficiality could be a step towards extended cognition, as we discuss below. While animals tend to be to a certain degree autonomous and independent of the environment, plants are highly embedded in it.

Crucially, in the terms of signaling and communication, plants can use internal networks (such as hormones or electrical signals) or the outside environment of the air or the soil, which would not be treated any differently from the plant’s internal networks.[3] Indeed, when we consider the volatiles in the air that convey information across the plant’s crown, or the rhizosphere that has physico-chemical properties highly modified by root exudates, or even the interaction with mycorrhizal fungi that extend enormously the surface area of the roots, it is hard to tell a plant apart from its environment. In other words, externally released exudates or volatiles perform essentially the same function as internal signaling networks of the plant. Likewise, plants that reproduce sexually will deploy non-plant actors, such as pollinating insects, birds, air currents, etc., to spread their

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[1] If we consider the behavior of roots individually, they appear mostly heterotrophic and consequently need to move to find nutrients, and they explore the environment in a fashion that resembles that of worms (except that their movements are achieved mostly by growth, and not displacement). This similarity was noted already by Darwin and Darwin (1880). See Baluška et al. (2006) for a discussion on the topic. We thank one anonymous reviewer for this observation.

[2] Interestingly, there are animals that evolved a sessile lifestyle. In these cases, they were submitted to similar evolutive pressures as plants, leading to similarities in their anatomies like modularity, little specialization of organs, and colonial nature. Examples include corals, sea sponges, hydrae, and bryozoans.

[3] After all, assuming the continuation of vegetative growth, parts of the growing plant will be there where the air or the soil around it are at this very moment.

**Fig. 1** A simplified representation of the body organization of a typical animal (beetles comprise 25% of all known animal species, Zhang et al. 2018). Animals are likely more integrated internally than externally, possibly having more channels of communication between elements of their bodies than between these elements and the environment. Besides, the most important channels of communication between animals and the world are concentrated in the head, where we find the brain, eyes, antennae, mouth, nose, ears, etc., or the extremities of their bodies. Black dots and lines represent elements of the animal body with their respective connections. Yellow dots and lines, elements and variables of the environment and their respective connections. Solid lines represent relations constitutive of the cognitive systems. Dashed lines represent relations between or with elements in the environment. Created with BioRender.com. (Color figure online)

genetic material. On these occasions, non-plant actors similarly figure as an extension of the plant outside its current embodied limits.

It may well be that the body organization of animals facilitates introspection, because they are likely more connected internally than externally, i.e., they seem to have more channels of communication between different parts of the body than between the body and the external world. For example, internal organs like the liver, kidneys, pancreas or heart have no direct contact with the environment, but influence and are influenced by the whole body. This could be illustrated by the systemic effect the adrenal glands have in the entire body through the release of adrenaline, from accelerating heartbeat to dilatating pupils, from regulating emotions to consolidating long-term memory (Brown et al. 1979; Cahill and Alkire 2003; Mezzacappa 2010). Another curious example is visual system processing: at least in mammals and birds, most of the stimuli for perceiving and processing visual information come from the brain itself, and not from the environment (Varela et al. 2016; Lev-Ari et al. 2022). What we see is directly related to what we are prepared to see due to previous experiences and current circumstances. We must have the relevant structures, or "schemata" (usually, networks in the brain, confirming Immanuel Kant's hypothesis of a priori cognitive structures), prepared to accept optic stimuli from the environment and retrieve information from it (Neisser 1976).

Plants, on the other hand, present more channels of communication between the modules and the external world than among the modules themselves. Although hormones do influence the whole plant body, there is no centralization in their synthesis. An exception could be the role of apical dominance in some herbaceous or young plants, but usually, hormones are produced by many modules at the same time, and as a result primarily of their interaction with their immediate environment (Martín-Vertedor and Dodd 2015). Consequently, whole-plant behavior emerges from the behavior of all the

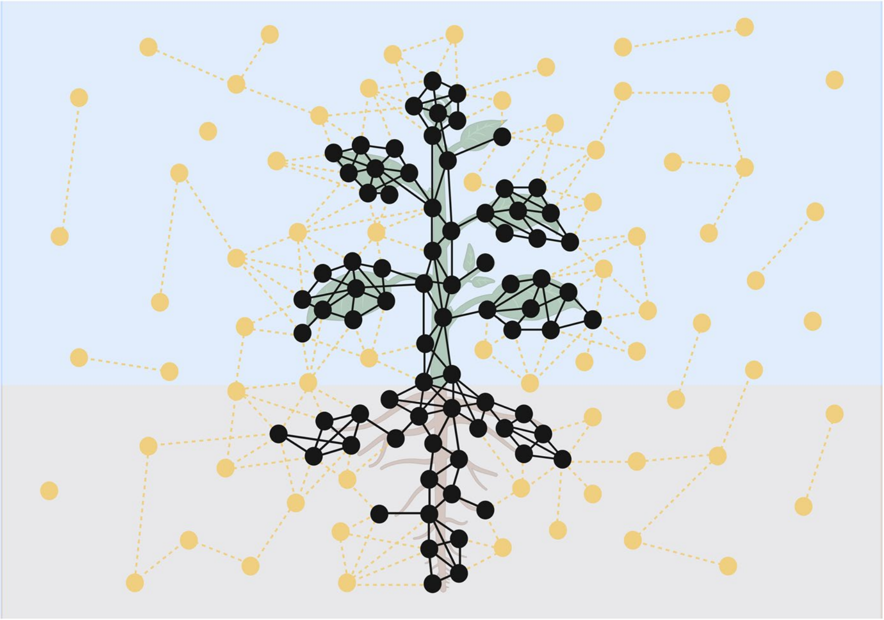

**Fig. 2** A simplified representation of the body organization of a typical plant. Their modular constitution implies that there are more channels of communication between the elements of the modules and the elements of the environment than with other modules. It does not mean that plants are less coordinated physiologically—as few as they might be, physiological connection among the modules are important to the coordination of behavior across the plant body (e.g., Falik et al. 2006). However, every module is far more autonomous in its behavior and interaction with the world than the "modules" that constitute the typical animal body. Black dots and lines represent elements of the plant body with their respective connections. Yellow dots and lines stand for elements and variables of the environment and their respective connections. Solid lines represent relations constitutive of the cognitive systems. Dashed lines represent relations between or with the elements in the environment. Created with BioRender.com. (Color figure online)

modules interacting with their immediate environment and from what is communicated between them (de Kroon et al 2009; Lüttge 2019).

Nevertheless, the distinction between animal and plant bodies does not mean that animals are more likely than plants to engage in cognitive processes. In fact, the cardinal mistake of theories of cognition is to equate thinking with introspective thought and consciousness with an invisible "inner container" for experiences, memories, and anticipations, among other components of psychic life. Cognition does not equal consciousness, and many, if not most, of our cognitive processes are unconscious to what we call *us* (Reber and Allen 2022). It is high time to shake off such dogma and to reconsider EPC in line with the three senses of the "extended" and elements of plant anatomy and physiology, as outlined above.

## 4 Implications of extended plant cognition (EPC)

Succinctly put, there are five main implications to the theory of EPC, with its locus not only on the living surfaces of a plant, but also and especially at the interfaces of the plant, its environment, and other—vegetal and non-vegetal—forms of life.

(a) As it is currently conceptualized, the information-processing model is inapplicable to extended plant cognition.

The model that explains cognition as information-processing solely in the brain is shown as inapplicable for several reasons:

a. If external networks and actors perform the same kinds of function as internal ones, situationally or occasionally integrating parts of a plant among themselves and with the outside milieu, then the "system" that would do the work of processing information is irreducible to a plant.

b. Furthermore, the essential instability in the inner/outer distinction in plants disturbs the distinction between inputs and outputs, required by any information-processing model.
c. As currently formulated within the paradigm of the conceptual and operational confines of closed systems, information storage and retrieval are likewise unworkable when the interiority, in which information would be stored and from which it would be retrieved, is not assured.

(b) The minimal unit of EPC is the plant + its environments (above and below ground).

The most fundamental question is not *What is cognition and its different types?* but *Who is the cognizer?* (With this, we propose a basic re-orientation toward plants as subjects, akin to the Kantian 'Copernican turn' in philosophy concerned with human reason, even though the limits of this subjectivity go well beyond the physical body of a given plant.) The unit of plant cognition is not a plant of a given species with its particular genetic make-up as an isolated specimen, but the plant + its immediate environment. This would be the strong sense of EPC. Its weak sense would be to start with the plant as a basic unit and only subsequently to add its interactions with the immediate environment(s) and representatives of other biological kingdoms and species.

(c) EPC is thinking with the environment, a co-thinking or a co-cognizing.

This follows from (b) and means that both organic and inorganic elements in a plant's environment are not mere tools for the accomplishment of its goals but synergic participants in the process of cognition. Housing, if only intermittently, airborne and belowground biochemical exudates of plants, the environmental milieu and its inhabitants who collaborate with plants are much more than the surrounding space, populated by other organisms. Rather, the space between an animal using sonar signals for navigation and the surfaces from which these signals bounce back, or between a root and an underground obstacle which serves as a barrier for the accumulation of biochemical exudates, is inseparable from the bodies of the animal or the plant within their respective trajectories of dislocation and growth. This intermediate space is a dynamic glove body or a second body, which is the site of extended plant (and animal) cognition.

(d) Overall, the decentralized equivalent of the central nervous system in plants is not another internal network but the conjunction of internal and external communication pathways, that is to say, of plants + not-plants.

Hence, the very idea of communication needs to change in tandem with that of cognition. Rather than a "mere" exchange of information between separate agents, who in their core remain unaffected or unaltered by the exchange, communication is the "connective tissue" of extended cognition. In the case of plants, the phenomenon of eavesdropping in self-signaling, for instance, would mean that the interface of plant self and non-self is the site of extended cognition. Similarly, transition zones around the root apex, where the richest cross-kingdoms interactions take place, are sites of extended cognition.

(e) The exceptional character of the sense of touch, as well as temperature and electrical sensing, scattered throughout the living extension of both plants and animals highlights their importance to extended cognition.

While acknowledging fundamental divergences between plant and animal modes of existence, body organizations, etc., we should not forget the overlaps between them, the overlaps that have the potential to become a shared physiological basis for extended cognition. Already Aristotle rightly noted that the organ of touch is not the hand; rather, it is all of skin, the entire sentient surface of the body (Aristotle 1975, p. 423a). The outward layer of the animal body is, in this sense, similar to that of plants. It is an organ that is decentralized, dispersed, and multifunctional: breathing through the pores, having photosensitivity, and thermal sensitivity, among others. Similarly, animals have free nerve endings scattered all over the skin in order to sense touch and temperature. Many fish and sharks have specialized structures in their skin to perceive electrical fields in the environment, like the ampullae of Lorenzini (Crampton 2019). To further study the interfaces that constitute extended cognition, it is, therefore, paramount to pay close attention to the unique qualities of the sense of touch, temperature, and electrical sensing, where these interfaces are anatomically and physiologically possible.

As for specific biochemical and physiological mechanisms, EPC is proposed to happen via four main channels: root exudates, root microbiota, mycorrhizal fungi, and volatile organic compounds (Parise et al. 2020, 2023). This list is not exhaustive, since other forms of extended cognition could be discovered (i.e., through the use of sound or ionic currents around root tips, see Gagliano et al. 2013; Baluška and Mancuso 2013). Below, we discuss some case studies as examples of how EPC may operate.

## 5 Test case of EPC (A): self-inhibition of root growth

Many plants release root exudates that, at certain concentration, become toxic to the plant itself or conspecifics (Singh et al. 1999; Wu et al. 2007; Asaduzzaman and Asao 2012). One hypothesis to explain this self-toxicity is that exudates help plants to distribute their roots in the soil more efficiently, something already demonstrated in previous studies (Falik et al. 2005; Semchenko et al. 2008; Caffaro et al. 2011). Root exudates can also cue plants to match root and shoot growth to the soil volume available (Wheeldon et al. 2021). Falik et al. (2005) studied the interaction of pea plant roots with the exudates they produce. They grew plants with the roots surrounded by nylon strings and observed that root tips would stop growing and even wither in the vicinity of the strings. The researchers hypothesized that root exudates would be mediating this effect. Then, Falik and colleagues applied activated charcoal or potassium permanganate behind the nylon strings. These substances would absorb and inactivate the exudates. The result was that, in the effective absence of exudates, the roots grew towards the nylon strings as if they weren't there. In other words, the removal of exudates inhibited the plants' capability of perceiving obstacles around the roots: the plants rely to a great deal not on their internal physiological/cognitive processes, but on an external process meant to detect obstacles around. This is remarkable because the ability to perceive objects in the case of pea plant root tips happens from the outside (through the build-up of ultimately toxic root exudates). But the outside is molded by the interaction of plant + immediate environment, the basic unit of EPC. The process is entirely different from the typical notion of self-inhibition, where blocks, restraints, or negative obstacles to a given behavior are erected inside this self, precisely as the realm of subjective interiority.

## 6 Test case of EPC (B): soil-borne legacy through root microbiota

Beyond their involvement in perceiving the environment around the roots, root exudates have a plethora of roles in plant biology, from lubricating the surface between the epidermis and soil particles to mineralizing nutrients (Bais et al. 2006; Badri and Vivanco 2009). Additionally, depending on their needs, plants can actively modulate and manipulate the soil microbiota by secreting different chemical substances like triterpenes, amino acids, long-chain organic acids (with more than six carbon atoms), nucleotides, and coumarins that promote or inhibit the growth of soil bacteria, altering significantly the composition of the rhizosphere's microbial community (Yuan et al. 2018; Zhong et al. 2022). The altered community can encode the memory of events the plant has suffered, like diseases and abiotic stresses, and helps the plant to endure and overcome these stresses if encountered again. This phenomenon is called *soil-borne legacy*.

Researchers who study this phenomenon are quite clear that modulation of root exudates' chemical composition is an *active* process controlled by the plant (Huang et al. 2019). This intention-driven interaction with the environment necessarily comes after an assessment of the plants' state. Once the microbiome is altered, this new community serves to encode the memories of past events, such that a repeated interaction with the plant changes how it endures similar stresses as those suffered in the past. We could say that the altered microbiota form an exogram (Sutton 2010): a physical representation of a past event stored outside the plant's body, its meaning only emerging when the plant interacts with it. This kind of memory is at odds with the conventional view of memory as an internal storage system, with parts to be retrieved and exteriorized whenever needed. Here, the memory of the plant is situated between the plant and its belowground environment, together with which it makes up the unit of cognition. Rather than an internal archive of past experiences, the memory connected to soil-borne legacy is a cross-species, cross-kingdoms event, material and ideal at the same time.

## 7 Test case of EPC (C): plant roots and mycorrhizal fungi

Mycorrhizal fungi are fungi that enter into associations with plant roots forming a symbiosis called mycorrhiza. This is a mutualistic symbiosis in which fungi retrieve nutrients from the soil and deliver them to the plant, which obtains carbon and lipids in return (Smith and Read 2008; Jiang et al. 2017). The connection of plants with these fungi is so intimate that they are often said to be an extension of the roots (Francis and Read 1994; Cheng et al. 2016). This ‘extension’, we argue, goes beyond the physical meaning intended by the authors, and is cognitive as well.

The principal aim of cognition is securing survival, which includes foraging and solving problems. The hyphae of mycorrhizal fungi do just this. In recent years, research has shifted from studying the foraging strategy of roots individually to studying how plants and mycorrhizal fungi forage together. It has been discovered that plants sometimes delegate to fungi the task of finding and absorbing nutrients, especially when they cannot forage for themselves (Tibbett 2000; Tibbett and Sanders 2002; Rosling et al. 2004; Eissenstat et al. 2015). Studies with both temperate and subtropical plant species have shown that there is a *functional complementarity* between the roots and mycorrhiza when foraging. Particularly, species that have thick absorptive roots have less precision when foraging with their roots than species with thin roots (Chen et al. 2016; Cheng et al. 2016). To overcome the lack of precision, thick-rooted species rely more on mycorrhizal fungi to forage for them, proliferating hyphae instead of roots (Eissenstat et al. 2015; Liu et al. 2015; Cheng et al. 2016). Fungi use their sensory apparatuses to find nutrients in the soil, but their actions are backed by the feedback plants provide through the delivery of carbon. In effect, when fungi do not provide plants with nutrients, the roots halt the supply of carbon and decrease colonization (Kiers et al. 2011; Yazici et al. 2021), and when fungi find a patch rich in nutrients, they can mobilise part of these nutrients to hyphae in poorer patches to increase the rewards from the plant in that area (Whiteside et al. 2019). Therefore, if we are to talk about foraging in plants—seeing that foraging is a behaviour that requires cognitive processes like decision-making, valence, and goal-oriented actions—it is impossible to separate plants and fungi. Who forages is neither the plant nor the fungi alone, but the plant + fungi unit. And who cognizes is, similarly, neither the plant nor the fungi alone, but the plant + fungi unit along with the patches of belowground environment they inhabit.

## 8 Test case of EPC (D): volatile organic compounds

Constitutively and as a result of biotic or abiotic stimuli, plants release volatile organic compounds (VOCs) into the air. These organic molecules are released by the leaves and ensure rapid exchange of information between branches of a plant, when communication by other, internal, channels would be dramatically less effective. Quite often, two leaves are rather close to one another, but, when dealing with different branches, communication through hormones or electrical signals could take hours or days. Besides, in a decentralized system, information emitted by one leaf or group of leaves would have to travel all the way down the branch until the stem, move to the other branch, and climb it until its extremity. There is too much room for loss of information along the way, and furthermore, if we consider the time it would take to complete the journey, it could be too late (a locust would jump from one leaf to another far quicker than the information about herbivore attack would take to reach distal leaves, which would be caught off guard). VOCs are the way plants worked this out (Frost et al. 2007; Heil and Karban 2010). Upon a stimulus, plants release a bouquet of substances that travel through the air, shortcutting physiological constraints and ensuring the communication with other modules in the same plant. In this way, they secure, for example, the priming of leaves and branches to future herbivore attacks, and synchronize fruit ripening, in the case of ethylene (Heil and Silva-Bueno 2007; Karban

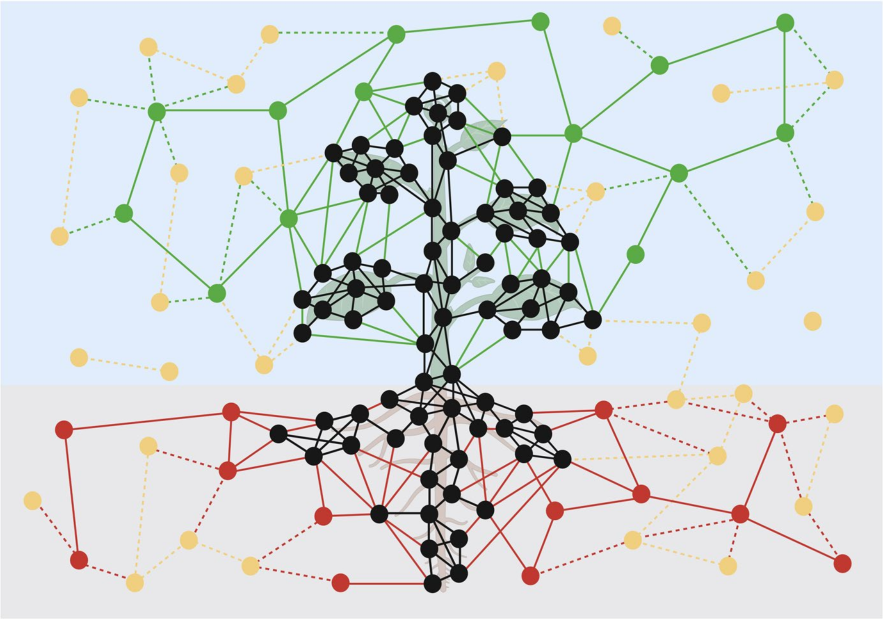

**Fig. 3** The bodily structure of plant cognition is rather different when we take into account its extended dimension. When plants fill the air with their volatiles (green), they create new channels of communication that shortcut distances imposed by their modular structure, increasing the cohesion of all the modules and the possibilities of interacting with the world. Likewise, they modify the soil with root exudates, alter the microbiota in the rhizosphere, and sustain mycorrhizal networks (red). Black dots and lines represent elements of the plant body with their respective connections. Yellow dots and lines, elements and variables of the environment and their respective connections. Solid lines represent relations constitutive of the cognitive systems. Dashed lines represent relations between or with the elements in the environment. Created with BioRender.com. (Color figure online)

et al. 2014; Alexander and Grierson 2002; Ságio et al. 2014; Moreira and Abdala-Roberts 2019). Throughout the course of evolution, plants employed this system to communicate with other plants and also animals and other organisms (Heil 2014). Communication per se does not imply, necessarily, cognition. Communication is, putting it simply, the exchange of information between systems (Karban 2015). Therefore, even non-cognitive systems like personal computers or cell phones can exchange information. However, communication is at the foundation of cognitive processes, because for them to happen the exchange of information is necessary, and it is one in which the parties exchanging it are fundamentally affected. In the case of plants, the exchange of information between modules is greatly facilitated by VOCs—and that is how plants extend their cognition through this mechanism—but we do not consider communication between plants necessarily as extended cognition, although not denying this possibility.

Cognition underlies problem-solving mechanisms, and one of the most important problems plants face is herbivore attacks. Several studies (reviewed in Heil and Karban 2010; Karban et al. 2014; Karban 2015) have demonstrated that, when under attack by herbivore insects, plants release herbivore-related VOCs that inform other parts of the same plant (or plants nearby) of the threat, inducing them to prepare defenses such as expressing defense-related genes, synthesizing chemical substances aimed to deter herbivores, and increasing production of extrafloral nectar and VOCs that attract predators of the herbivores who attack them (Heil and Karban 2010). In this fashion, plants can prevent further herbivore damage to a significant extent. The production of VOCs is not hardwired in the sense that every stimulus produces a corresponding blend of VOCs, as though this correlation were genetically encoded. Quite the opposite: the identity of the herbivore, the nature of the damage, the ecological context, and other biotic and abiotic, endogenous and exogenous factors influence the message that is delivered (Moreira and Abdala-Roberts 2019).

Interesting examples are the studies with *Artemisia tridentata* and *Phaseolus lunatus*, which demonstrate that, within the same species, VOC bouquets encoding the same messages present regional differences, and these differences can impair communication between conspecifics that do not speak the same "chemical dialect" (Karban et al. 2016; Moreira et al. 2016). In other words, the same message can be encoded in different sets of VOCs, and their meaning is not entirely genetically determined, but is also context-dependent (Moreira and Abdala-Roberts 2019).

Thus, available evidence suggests that volatiles play a role akin to internal networks of communication such as electrical signals, calcium waves, reactive oxygen species, and hormones (not forgetting that ethylene is a volatile plant hormone). Information deriving from biotic or abiotic stresses can be transmitted by any of these routes, and if we adopt a loose functionalist perspective, there is no objective difference between any of these channels of communication when they cause the same effects. Plants cannot be separated from their volatiles, and their crowns are constantly immersed not only in the oxygen and humidity perspiration, but also in an invisible cloud of info-chemicals created by the plants themselves. This means that the structure of the entire tree is not a hierarchical arrangement, dependent on the central trunk (Deleuze and Guattari 1987), but a rhizome-like assemblage where external channels of communication by means of VOCs released into the air are at least as important as the inner channels passing inside the branches.

## 9 Conclusions

Here, we discussed the concept of EPC and its implications for plant biology. The sessile and modular nature of these organisms molded the way they perceive and act in the environment, as well as how they deal with information. Eventual limitations imposed by their body organization, however, can be partially overcome by actively intervening in and shaping the environment around them, which extends plant cognitive process.

With VOCs, root exudates, soil microbiota and mycorrhizal fungi, plants can extend far and wide their influence in the world, shortcutting distance constraints caused by their modular structure when communicating internally, increasing the surface of potential interactions with elements of the environment, storing information outside their bodies—information that is made accessible to other plants as well—, and communicating with distant plants and other organisms. In summary, the full realization of plant cognition is only possible with an environment that is both shaped by plants, and that shapes themselves (Fig. 3).

With this in mind, studies investigating EPC empirically should intervene in the mechanisms by which plants putatively extend their cognition, thereby establishing relations of constitutive relevance between the cognitive system and the elements in the environment to which it presumably is extended and extending (Parise et al. 2023). As discussed in detail elsewhere (Parise et al. 2020, 2023), a good way of investigating EPC would be intervening in the cognitive system, for example, by challenging plants with problems that require the use and manipulation of information to be solved (e.g., growing roots in mazes that force decision-making, or introducing herbivores, or pathogens that cause immunological memory), and observing how plants use elements of the environment to solve these problems. Subsequently, interventions in the same elements should cause an observable alteration in the cognitive system when solving the same or similar problems. In this case, activated carbon can be employed to study the importance of root exudates to spatial orientation (Mahall and Callaway 1992; Falik et al. 2005). Soil-borne legacy can be studied with application of synthetic exudates or substances (Yuan et al. 2018), and the application of exogenous or synthetic VOCs can be used to infer the importance of these molecules to efficient problem-solving and within-plant communication (Karban et al. 2016; Moreira et al. 2016). Finally, the use of different species or strains of mycorrhizal fungi, as well as transformed plants and fungi, could be employed to understand the role of mycorrhizal networks in plant cognition (e.g., Eissenstat et al. 2015; Liu et al. 2015; Cheng et al. 2016).

Despite the usefulness of such studies, we also underline the importance of thinking of plants and studying them in their natural contexts. It is almost a cliché to say that plant behavior in controlled, laboratory conditions may be much different from what is observed in the field. One of the reasons for this difference might be a disruption of the network of interactions constructed by the plant and represented in Fig. 3. Future research on plant performance, yield, or behavior, should take into consideration the possibility of plants extending their cognition, as discussed here.

As we have seen, cognition is inherent to life (Maturana and Varela 1980; Lyon et al. 2021). We should not talk about living organisms and their ecological interactions ignoring the cognition that sustains their behaviors. Therefore, if one wants to understand what a plant is, its cognitive processes must be considered. But if the cognition of plants is extended, what is a plant, after all? Plants are inseparable from their environments—environments that are carved by themselves to a great extent. Hopefully, future research will investigate plants through the extended cognition lens, seeing them, like in Fig. 3, as a network of relations and interactions that goes beyond bark and epidermis, throughout which there is a continuous flow of information modifying and reshaping the structure of the network itself.

Acknowledging the extended cognition of plants may have important implications in agriculture as well. Firstly, because the concept relates directly to plant stress. By altering the environment, plants create an eco-physiological niche that stores memory and buffers biotic and abiotic stresses (Galviz et al. 2019), especially through microbial soil-borne legacy and mycorrhizal associations (Gehring et al. 2014; Raaijmakers and Mazzola 2016; Pavithra and Yapa 2018; Bakker et al. 2020). It is known that soil microbial diversity is pivotal for the building of memories in the soil. The richer the diversity, the more possibilities of recruitment a plant has to shape its rhizosphere, resulting in memory effects (Raaijmakers and Mazzola 2016). The same goes for mycorrhizas, which are known to increase plant resistance to biotic stresses through the activation of plant immune system (Jung et al. 2012; Fujita et al. 2022) or by sheathing the root tips in the case of ectomycorrhizas (Marx 1971). It follows that soil health is inseparable from plant health and is crucial to providing plants with the tools to create their eco-physiological niches, or the cognitive niches, they need to endure stresses. Plant wellbeing is not a secondary issue, but one that is intertwined with soil health, sustainable agriculture, and the potential of agroecological practices that naturally enable these processes.

However, there are possible technological applications as well. If there is a physical extension of plants' cognition that helps them interact with the environment and resist stress, this should be adjustable to improve crop productivity. For example, the release of synthetic VOCs in the field could prime plants to better withstand drought or diseases. The design of soil probiotics with specific mix of bacterial taxa that either creates 'artificial memories' in the soil or facilitates the creation of exograms by the plants could also increase plant resistance to stresses, and should be considered (Bakker et al. 2020; Yang et al. 2023). It might also be interesting to consider the extended dimension of plants when phenotyping, for some plant species or varieties may be better equipped to create eco-physiological niches that promote their own growth and yield. These traits could be selected and bred to create cultivars that are better able to shape their environment, again aiming at higher resistance to stresses and higher productivity (Yang et al. 2023). The new challenges posed by climate change require original approaches in agriculture, and taking EPC into account can inspire new ideas to pursue food security, coupled with plant wellbeing.

Finally, in this paper we usually consider a single plant + its above- and belowground environments as a case study. Further intriguing questions are whether and how the networks of interactions in the extended cognitive system of a plant interact with the networks of other plants. If VOCs or mycorrhizal fungi shortcut the distance between modules, allowing communication between them and regulating their behaviors, what happens when they do it to other plants? (Karban et al. 2014; Gorzelak et al. 2015). Does the extended cognition of a plant stop at other plants, or does it extend to them? How would we see a forest in this case? These are promising questions that should be raised once we acknowledge the possibility and the actuality of extended plant cognition.

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**Conflict of interest** The authors declare no conflict of interests.

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