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Plant Cognition—A Methodological Primer: Theories, Methods and Challenges

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ABSTRACT

Part I: What counts as cognition, and how can it be studied in organisms without nervous systems? The emerging field of plant cognition confronts these questions by integrating philosophy, plant science and comparative psychology. This article provides a methodological primer on the field. We first survey major theoretical approaches—computationalist and representationalist, radical embodied, and behaviour-first—and consider how they might be integrated. We then examine methodological strategies, from comparative experimental paradigms to the role of philosophy in clarifying concepts and guiding research design. Finally, we address key epistemic challenges, including replicability, anthropomorphism and confirmation bias. Taken together, these discussions establish a conceptual and methodological foundation for plant cognition research. A companion article, Plant Cognition—An Empirical Primer, complements this survey by reviewing the empirical evidence and its philosophical implications.

1 | Introduction

The study of plant cognition sits at the intersection of empirical research and philosophical inquiry, challenging long-standing assumptions that restrict cognitive capacities to animals. In the past two decades, studies have explored plant decision-making, anticipatory behaviour and communication, among other candidate capacities (for a review, see Segundo-Ortin and Calvo 2021). These findings raise fundamental questions about what counts as cognition and whether cognitive abilities require neural structures (Artiga 2024; J. Lee 2023; Leonetti 2025; Linson and Calvo 2020). As a result, plant cognition has become the focus of an interdisciplinary debate spanning plant science, cognitive science, philosophy and comparative psychology. Whereas some researchers argue that plant behaviours display hallmarks of cognition (Trewavas 2003, 2014; Calvo and Trewavas 2021; Calvo and Keijzer 2009; Calvo Garzón and Keijzer 2011), others insist they can be explained without invoking cognitive processes (Adams 2018; Figdor 2024).

This paper provides a methodological primer on plant cognition, integrating philosophical analysis with key empirical developments. Section 2 surveys major theoretical frameworks—computationalist and representationalist, radical embodied and behaviour-first approaches—before outlining how each might apply to plants. Section 3 turns to methodological strategies, from comparative psychology to the contribution of philosophy. Section 4 addresses key epistemic challenges, including the replicability crisis, anthropomorphism and confirmation bias. Finally, Section 5 concludes by highlighting the broader significance of these conceptual and methodological issues, whereas a companion article, **Plant Cognition—An Empirical Primer**, reviews the empirical state of the art and its philosophical implications.

2 | Theoretical Approaches to Plant Cognition

What counts as cognition remains a central question in cognitive science and philosophy of mind (Allen 2017; Bayne

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et al. 2019), making it difficult to settle the question whether plants are cognitive or not. Consequently, extending cognitive categories to plants remains contested, with some scholars regarding attributions of cognitive capacities to plants as metaphorical or merely pragmatic (Figdor 2024; Adams 2018).

In this section, we survey three major approaches—computational/representational, radical embodied and behaviour-first—highlighting their criteria for cognition and their implications for plants.

2.1 | Computationalist and Representationalist Views

On the cognitivist view, cognition is computation over internal representations, either symbolic (Newell and Simon 1972) or sub-symbolic (Rumelhart and McClelland 1986). According to this view, plants are cognitive if they build and manipulate models of the world that guide behaviour. Therefore, explaining plant behaviour would require specifying how those representations are encoded and computed by the plant.

Whereas computational theories usually presuppose neural substrates (often centralised), which makes them ill-suited to highly decentralised aneural organisms such as plants, there are nowadays computational proposals aimed at saving this obstacle. For instance, Davis et al. (2024) propose modelling plant behaviour and decision-making as a consequence of distributed, decentralised computation. They suggest that 'a unified [behavioural] output [...] is achieved through aggregation using an algorithm' (746). This approach, however, leaves it open the question whether plants use symbolic or analogue representations, or where do plants compute, thus raising the question of *what type of computing system* a plant would be, if any. Critics object that plants lack representations altogether, thus concluding that they do not qualify as cognitive beings (Adams 2018; Aizawa 2014).

Two cautions follow. First, whether plants deploy representations is an open empirical question and claiming that plants lack them begs the question. Second, treating the computational theory as an a *priori* criterion for cognition, rather than as one explanatory hypothesis among others, risks conflating *explanandum*, the cognitive capacity we aim to explain, with *explanans*, a representational mechanism (Ramsey 2017; Allen 2017; Segundo-Ortin and Calvo 2019). As we see it, the question of whether plants have cognitive abilities should be addressed independently of the cognitive mechanisms that underlie those abilities (J. Lee 2023).

This controversy reflects a wider debate in the philosophy of cognitive science about whether computation necessarily entails representation. Some authors argue that computational explanations can be given in purely mechanistic terms, without positing representational content (Piccinini 2007; Egan 2010). Others maintain that computation is inseparable from representation, making representational content indispensable. Situating plant cognition within this dispute highlights its relevance beyond botany: the plant case sharpens the question of whether flexible behaviour requires representational mechanisms at all. In this sense, the issue intersects with discussions of minimal cognition (Brancazio et al. 2020), where the *explanandum* is adaptive behaviour itself, and the explanatory challenge is to determine what organisational principles or mechanisms underlie it.

2.2 | Radical Embodied Approaches

In contrast to cognitivist models, radical embodied theories reject the necessity of internal representations and computations for cognition. Despite their internal diversity, these approaches share a core commitment: cognition is not something that happens solely inside the brain (or its analogues) but emerges from the dynamic coupling between an organism's bodily form, its sensorimotor capacities and the environment (Barandiaran and Moreno 2006; Van Duijn et al. 2006). This perspective shifts explanatory emphasis away from internal representation manipulation and toward the real-time sensory–motor interaction between organism and world. Moreover, since these frameworks downplay the need for of a nervous system, they might be particularly well suited to the study of plant cognition.

A prominent radical embodied framework that has been applied to plants is ecological psychology (see Calvo 2016; Carello et al. 2012; Calvo et al. 2017; Frazier 2024; J. Lee and Ponkshe 2024; Ferretti 2024). According to ecological psychology, organisms perceive and coordinate their actions without mediating computations (Gibson 1979; Segundo-Ortin and Raja 2024). Information in the ambient energy arrays (e.g., light, volatile organic compounds, mechanical vibrations etc.) specifies the *affordances* (opportunities for action) in the environment, enabling organisms to control behaviour directly on the basis of detected information.

This framework has been applied to explain how climbing plants such as vines close the gap to a nearby support (see Calvo et al. 2017). The *tau hypothesis* proposes that the vine relies on an informational variable ('tau') specifying the time-to-contact with the support (D. N. Lee 2009). 'Closing the gap' (Pepping and Grealy 2007) refers to the process by which growth is dynamically adjusted to ensure successful contact. By monitoring the changing time-to-contact and modulating growth rate accordingly, the plant perceptually guides its movement toward a goal. As Lee puts it, '[m]oving purposively to contact something entails perceptually guiding the closure of the gap between the effector and the goal' (D. N. Lee 2014, 48). On this view, the vine's circumnutatory growth movement is not a mechanical reflex but a form of adaptive perceptually guided behaviour that parallels principles of goal-directed movement described in animals (D. N. Lee and Reddish 1981).

Even though the hypothesis has yet to be empirically substantiated, and the physiological mechanisms by which plants might detect such information are not yet fully understood, the example illustrates how an ecological perspective can reframe plant behaviour in non-cognitivist terms. Rather than treating directed growth as the output of internal representations, the ecological approach asks whether plant movements are *perceptually guided* by environmental *affordances* (Carello et al. 2012). Nonetheless, this shift introduces new challenges: researchers must specify what informational variables plants could plausibly detect and how such detection might be realised physiologically. Until a clear account of plant perception is established, perceptual guidance in plants should be treated as a working hypothesis, one that requires sustained empirical and theoretical development.

Another radical embodied approach relevant to plants is enactivism. Enactive theories hold that cognition arises through the ongoing regulation of sensorimotor coupling, where the organism brings forth its own meaningful world through interaction (Varela et al. 1991). A distinctive claim is the mind–life continuity thesis: the organisational principles underlying basic life processes—self-maintenance, autopoiesis and adaptive regulation—already constitute the roots of cognition (Thompson 2010; Maher 2017). It follows that even simple organisms—and perhaps plants—exhibit a rudimentary cognitive organisation insofar as they actively regulate themselves in changing environments.

Both ecological psychology and enactivism emphasise that cognition is not confined to brains or nervous systems but is realised in the dynamic coupling of organism and environment. Whereas ecological psychology highlights the informational structure available in the environment for guiding behaviour, enactivism stresses the autonomous organisation of the organism as it enacts a world. For plants, these emphases can be complementary: plants detect ecological information (in the form of light gradients, chemical cues and mechanical stimulation) through their diverse sensory capacities and exploit it to maintain their self-organising dynamics (growth regulation, resource allocation and stress responses). Taken together, radical embodied theories provide a conceptual toolkit that makes plant cognition intelligible without assuming internal representations or neural analogues. They redirect explanatory effort from internal computation toward specifying what kinds of ecological information plants might be sensitive to, and how their bodily organisation enables them to act adaptively in real time.

Critics of radical embodied approaches, however, argue that they are overly inclusive, blurring the distinction between cognitive and non-cognitive phenomena. For instance, Figdor (2024) warns that if every instance of adaptive responsiveness qualifies as cognition, the concept risks inflation and loses its analytic utility. Similarly, enactivism is often accused of conflating physiological regulation with genuinely cognitive organisation, erasing distinctions that matter for explanatory purposes. Along the same lines, Aizawa (2014) claims that ecological psychology overlooks the difference between behaviour and the cognitive processes typically invoked to account for it. Defenders of radical embodiment respond that the challenge is not to police a sharp boundary but to understand cognition as a spectrum grounded in degrees of organisational complexity (Di Paolo et al. 2017), admitting that some behaviours can also be part of the processes that allow organisms to solve cognitive tasks.

2.3 | Behaviour-First Approaches

Echoing recent debates about consciousness in non-human animals (see Birch 2022), we can opt for a minimal assumption or ‘theory light’ framework, approaching cognition from the outside in. Instead of beginning with theories about internal representations or organisational principles, it treats specific observable behaviours as the primary criteria for attributing cognitive abilities such as learning, decision-making and the like (Godfrey-Smith 2017). On this view, if an organism reliably produces adaptive, context-sensitive responses that display the hallmarks of cognition, it is legitimate to describe those responses in cognitive terms, without committing to a specific theory of cognition or making assumptions about the underlying architecture. Paraphrasing Dacey, the assumption is that ‘we could identify [cognitive] behaviours and sort out the theory later’ (2025, 182).

For defenders of this strategy, evidence for cognition in plants comes, for instance, from foraging decisions in roots (Novoplansky 2019), shade-avoidance strategies in shoots (Aphalo et al. 1999; Pierik and De Wit 2014) and even reports of associative learning in conditioning paradigms (Gagliano et al. 2016). Such cases suggest that plants may exhibit behavioural flexibility that merits cognitive interpretation (see the companion article, Plant Cognition—An Empirical Primer).

However, critics caution that behavioural complexity does not automatically imply cognitive complexity. For instance, Schulte (2024) argues that whether plants qualify as cognitive depends on the degree of information-processing complexity underlying their responses, not simply on their observable flexibility, and rejects ‘easy arguments’ that infer representation, or cognition, more generally, from adaptive responsiveness alone, warning that such inferences risk overextension. This relates to the challenge of specifying the mark of the cognitive: which kinds of flexibility should count as cognitive, and which remain in the domain of physiology? Without principled boundaries, behaviour-first approaches may inadvertently expand the concept of cognition too far.

Nevertheless, the behaviour-first strategy has pragmatic advantages. It anchors inquiry in observable, testable phenomena and avoids premature commitments about internal mechanisms. It also creates a level playing field for cross-kingdom comparisons: organisms as diverse as slime moulds, invertebrates, and plants can be evaluated according to the same behavioural benchmarks. Yet the very diversity of behaviours invoked—decision-making, anticipation and communication—shows the need for philosophical clarification. Without a careful conceptual framework, the term ‘cognition’ risks being applied inconsistently across cases, giving rise to double standards (see Section 3). This is where a comparative psychology perspective proves crucial (see Section 3.1): If, for example, a plant behaviour is to be described as decision-making, it must exhibit the signatures or benchmarks (such as flexibility, sensitivity to trade-offs etc.), that comparative cognition research already uses to evaluate decision-making across taxa, from microbes to animals (Shettleworth 1993; Halina 2023; Beran et al. 2014).

In sum, behaviour-first approaches provide a useful heuristic for expanding the comparative study of cognition. They foreground what organisms do rather than what structures they have. However, their ultimate value depends on developing sharper criteria for when behavioural flexibility warrants a cognitive interpretation and how such interpretations can be empirically distinguished from purely physiological accounts.

2.4 | Embracing Pluralism

None of the frameworks considered—computationalist, radical embodied or behaviour-first—offers a complete account of plant cognition on its own. Each highlights a different dimension: representational models stress internal information processing, embodied theories emphasise real-time organism–environment coupling, and behaviour-first views underscore the importance of observable flexibility. As we see it, the challenge is not to crown one approach the winner but to articulate how these perspectives can complement one another.

One productive path is to adopt a pluralist and prediction-driven strategy. Behaviour-first approaches identify candidate phenomena—such as decision-making, anticipation or communication—that call for explanation. Ecological and enactive theories then propose how these behaviours might be organised without representations, by specifying the informational variables and self-regulatory mechanisms available to plants. Computational models, in turn, can test whether plant signalling networks perform functional roles analogous to those in neural systems, offering a bridge between abstract information-processing accounts and embodied dynamics.

Integration also clarifies burdens of proof. Strong claims about plant cognition should survive replication, rule out simpler physiological explanations, and generate novel, testable predictions. In practice, this means triangulating across behavioural signatures (flexibility and plasticity), ecological analyses (affordances and perceptual variables), and mechanistic models (signalling pathways and systemic coordination). Where these converge, the case for cognition in plants is strengthened.

In this way, pluralism is not a retreat to vagueness but a commitment to explanatory adequacy. By combining the strengths of each framework, researchers can move beyond entrenched dichotomies—representation versus non-representation, neural versus aneural and behaviour versus physiology—and instead pursue a more integrated science of plant cognition.

3 | Methods in the Study of Plant Cognition

Beyond theory, progress in plant cognition depends on methods that combine comparative psychology, plant science and philosophy. Because plants lack a nervous system and operate on different timescales, research requires tailored experimental designs, interdisciplinary collaboration, and careful conceptual framing. Nowadays, we are witnessing the productive collaboration of philosophers and cognitive scientists in comparative psychology, and the field of plant cognition should not be different: whereas scientists work to adapt protocols from comparative psychology, using behavioural and neurophysiological assays to probe decision-making, learning or communication, philosophers help refine questions, interpreting results, and uncover hidden biases.

Nowadays, we are witnessing the productive collaboration of philosophers and scientists.

3.1 | Comparative Methods

Comparative approaches offer a powerful framework for evaluating cognition across species. Just as comparative physiology has illuminated biological functions (e.g., rapid movements in *Droseraceae*; Williams 2002), comparative psychology can extend cognitive inquiry beyond animals (Abramson 2023). By analysing how diverse organisms perceive, process information and respond to their environments, researchers can identify cognitive patterns that transcend particular architectures.

A core challenge is tailoring and calibrating protocols so they respect species-specific traits while still enabling meaningful cross-species comparisons (Huey et al. 2002). The first step toward such calibration is constructing ethograms which are systematic catalogues of species' behavioural repertoire under natural and semi-natural conditions (Abramson 1994). Adapted to plants, ethograms can provide a structured framework for describing the full range of plant behaviours (Silvertown and Gordon 1989, for the plant behaviour framework). Besides, combined with detailed natural history observations, plant ethograms can establish behavioural baselines revealing patterns of variability, sensitivity and response timescales. These baselines are invaluable for designing species-specific experimental protocols, guiding the selection of appropriate stimuli and responses, and ensuring that cognitive assays in plants are both ecologically meaningful and methodologically rigorous.

In plants, where behaviours unfold far more slowly than in animals, techniques such as time-lapse imaging are indispensable for visualising growth and movement (Stolarz 2009; Stolarz et al. 2014). Critics sometimes argue that such methods distort plants by making their behaviour look 'animal-like' (Taiz et al. 2019). But as Shettleworth (2010) notes for early animal cognition debates, accusations of anthropomorphism can themselves reflect bias rather than methodological error, a caution equally relevant to plants.

Time-lapse methods are now paired with computational and imaging tools. Software such as *Plant Tracer* (Brenner 2017) quantifies growth trajectories, distinguishing between genotypes (e.g., wild-type vs. pgm-1 *Arabidopsis*, the latter showing reduced circumnutation and gravitropism; Guercio et al. 2019). Computer vision enables 3D reconstructions of climbing behaviours (Ruiz-Melero et al. 2024), offering new insights into the spatial organisation of movement. Meanwhile, machine learning models—such as the deep learning-based tracker developed by Mao et al. (2023)—have dramatically improved accuracy and speed in identifying movement patterns, even on non-specialist hardware.

Physiological-level data can enrich these behavioural studies further. For instance, real-time calcium imaging provides insight into intracellular signalling dynamics (Zhang et al. 2023), whereas MRI and PET imaging can be used to visualise carbon allocation and transport routes in growing root–shoot systems under realistic soil conditions (Jahnke et al. 2009). Together, these tools bring plant cognition studies closer to the standards of systems neuroscience.

It is worth noting that adapting classic animal cognition paradigms to plants requires careful modification. A case in point is Gagliano et al. (2016), where researchers modelled Pavlovian conditioning in peas by pairing blue light, as the unconditioned stimulus (US), with an airflow from fan, as the conditioned stimulus (CS). However, this experiment has been criticised for key methodological shortcomings, particularly the use of an opaque Y-maze, which prevented continuous observation of plant behaviour during the entire learning assay and imposed constraints on the conditioning procedure and its interpretation. Additional concerns include the inability to control the precise location of seedling emergence, which is critical given the maze's geometry; the absence of a single-subject design and the lack of finer control over airflow from the fan (CS)–light (US) measurements and their administration (Ponkshe et al. 2024). Such precision is particularly important in plant studies, as minor variations in stimuli intensity and spectral composition can substantially alter plant morphogenesis and physiology (see Cvrčková and Konrádová 2022, for a detailed discussion of how light-quality differences in Gagliano et al.'s original experiment and its attempted replication by Markel (2020a), may account for their divergent results).

Mathematical formalism is also important for comparative methods. For instance, Raja et al. (2020) applied dynamical systems analysis to plant nutation, revealing patterns consistent with goal-directed movement and endogenous control akin to those detected in human and non-human animals. Likewise, Schmid (2016) used risk sensitivity theory (RST) to model pea plants' anticipatory decision-making under dynamic and static nutrient regimes (Dener et al. 2016). RST predicts an inflection point at which it is rational to shift from a risk-averse to a risk-prone behaviour given a particular configuration of internal and external states of the system. Importantly, Schmidt and colleagues demonstrate that 'theories of decision making and optimal behaviour developed for animals and humans can be applied to plants' (Schmid 2016, R677).

In sum, comparative methods—if carefully designed—can help bridge the gap between plant and animal cognition research. As with the early days of comparative psychology, the key is to remain attentive to species-specific constraints without forfeiting the possibility of drawing meaningful comparisons that help us advance in our understanding of cognition across biological kingdoms.

3.2 | Why Plant Science Needs Philosophy

Tackling plant cognition requires a transdisciplinary effort that includes philosophy as well as other scientific disciplines within both plant biology and cognitive science (Calvo 2016). In our view, philosophy can contribute in different ways.

First, philosophical inquiry can help sharpening key notions, evidencing situations in which crucial concepts are being used differently across studies and theoretical frameworks. This conceptual clarification is crucial for ensuring that comparative studies are truly comparable, fostering more precise and theoretically grounded research.

Second, philosophers can play a pivotal role in uncovering hidden biases and methodological shortcomings in the research (see Section 4). Evidence of this are the philosophical work of scholars pointing out the detrimental effects of anthropocentrism, anthropomorphism, anthropectomy, and anthropofabulation in animal cognition research (Andrews 2020a, 2020b; Buckner 2013; Segundo-Ortin et al. 2026), the uncritical adoption of some hypotheses as 'null' by default (Mikhalevich 2015), the problematic practice of preferring Type-II (false negative) to Type-I (false positive) errors in comparative psychology (Andrews and Huss 2014), or the current replication crisis. Because plant cognition research is equally affected by these issues, the philosophical analysis just mentioned are equally useful in this field.

Third, as Brook (2009) argues, philosophers can have a substantive role both in generating new hypotheses by means of thought experiments, this is, 'imagined manipulations of imagined scenarios' (222), and interpreting the results in light of the competing hypotheses.

Finally, philosophy can encourage complementing mechanistic analyses with broader perspectives from evolutionary biology, ecology and developmental systems theory. Although cellular, biochemical and molecular analyses are indispensable for understanding how plants work, they may not, on their own, illuminate whether or how plants process information or interact with their environments in cognitively interesting ways. An integrative stance does not replace reductionist explanations but situates them in context, helping to explain how complex behaviours, including those potentially related to cognition, emerge from multiple-level interactions in biological organisation.

Philosophical perspectives have already shaped plant cognition debates. For instance, by questioning the assumption that cognition requires a nervous system, philosophers have expanded the theoretical landscape of comparative psychology (Calvo and Segundo-Ortin 2023). Likewise, classic issues such as other minds and multiple realisability (Putnam 1967) remain central: they bear directly on whether plant behaviour should be interpreted as cognitive or simply as non-neural adaptive intelligence.

In sum, advancing plant cognition requires an interdisciplinary synthesis of empirical work and philosophical analysis. By combining insights from plant biology, cognitive science and philosophy, researchers can develop more robust theories and methodologies, advancing the field beyond semantic disputes and toward a deeper understanding of intelligence in biological systems.

These considerations set the stage for a closer examination of some of the epistemic challenges that arise when studying cognition in plants, which we address in the next section.

4 | How to Study Plant Cognition?

The empirical study of plant cognition faces several methodological challenges. A central tension lies between laboratory and field studies. Laboratory work affords precise control over variables, reducing confounding factors and enhancing reproducibility. Field studies, by contrast, provide more ecologically valid settings in which natural behaviours and interactions can be observed, offering broader and more holistic insights into organismal behaviour and ecosystem dynamics. Ecological validity, however, comes at the cost of control: noise increases, and causal connection between variables becomes more difficult to establish.

A second issue is the heavy reliance on some plant models. Similar to the lab mouse and *Drosophila* in vertebrate and invertebrate animal biology, or WEIRD subjects—participants from Western, Educated, Industrialised, Rich and Democratic societies—in human psychology (Henrich et al. 2010), in human psychology, *Arabidopsis thaliana* is favoured in plant biology for its genetic tractability, short life cycle and rich genetic and genomic resources. But this convenience introduces bias: other species remain underrepresented, and unique biological processes risk being overlooked (Bolker 2012; Koornneef and Meinke 2010; Woodward and Bartel 2018). Moreover, findings from *Arabidopsis* in controlled environments may not generalise to plants in natural ecosystems, skewing data on plant behaviours (Meyerowitz 2001).

Finally, questionable scientific practices pose particular risks for a young and controversial field such as plant cognition. Responsibility lies not only with researchers but also with publishers, editors and reviewers. Common problems include (i) publication biases—favouring positive findings while neglecting null results, a serious issue when early claims require careful vetting (Fanelli 2012); (ii) lack of standardised methodologies, which hampers replication (Open Science Collaboration 2015) and (iii) the publish-or-perish culture, which prioritises output over rigour (Edwards and Roy 2017). The neglect of null results is especially problematic: in population genetics, for example, the Hardy–Weinberg equilibrium functions as a foundational null hypothesis, and confirming it is just as informative as detecting departures from it (Rohlfs and Weir 2008). In plant cognition, too, null results are critical checks that prevent premature claims from shaping the field. Without them, pressures have at times encouraged the dissemination of premature or irreproducible findings (see, e.g., Lobet (2017) in the context of the development of plant imaging techniques).

In the remainder of this section, we will focus on three specific problems which affect plant cognition research, undermining the reliability of findings in this emerging field: the replicability crisis, accusations of anthropomorphism and, finally, the pervasive effect of confirmation biases in the empirical studies.

4.1 | Replicability Crisis in Plant Cognition Research

The replicability crisis (Ioannidis 2005) —the widespread difficulty of reproducing scientific results (Atmanspacher and Maasen 2016; Fidler and Wilcox 2021; Guttinger 2020)—, has been especially visible in psychology (Coyne 2016) but extends to other fields, including plant cognition (Garcia-Simon 2021). As an emerging discipline, plant cognition must prioritise replication of foundational experiments to establish the reliability of controversial findings. This need spans all subfields, from plant electrophysiology to plant behaviour and ecophysiology.

Yet many plant studies have failed to replicate consistently, raising concerns about the reliability and validity of the reported findings. Contributing factors include small sample sizes, which reduce statistical power and increase variability; insufficient methodological detail; and limited data sharing, which prevents independent verification. Our own experience at the MINT Lab replicating plant learning studies (Gagliano et al. 2016)—for discussion of previous failures to replicate Gagliano et al.'s study (see Cvrčková and Konrádová 2022; Markel 2020a, 2020b; Gagliano et al. 2020)—revealed several deficiencies. To address these issues, we have proposed improvements for both direct replications (closely reproducing the original experiment) and conceptual replications (testing the same hypothesis with alternative methods; Schmidt 2009; Romero 2019), in order to determine whether plants can indeed learn by association (Garcia-Simon 2021; Ponkshe et al. 2024).

Addressing replicability is essential for distinguishing genuine phenomena from anomalies or anecdotal observations. By strengthening reliability, plant cognition research can move toward a more rigorous understanding of plant signalling and behaviour.

4.2 | Anthropomorphism

The hypothesis of plant cognition is often met with accusations of anthropomorphism, the unwarranted attribution of human cognitive capacities to non-human species. We agree that avoiding anthropomorphism is crucial, but, following Andrews (2020a, 2020b), we believe that the best safeguard is to take the scientific method seriously: we should ask whether attributing a cognitive capacity—such as learning, decision-making or communication—to plants is the *best explanation* for the available evidence.

At the same time, accusations of anthropomorphism may themselves reflect an anthropocentric bias. Anthropocentrism treats human cognition as the 'gold standard' against which other species are judged. Adams (2018) exemplifies this view in arguing that plants cannot display anticipatory behaviour, since anticipation (and cognition, more generally) requires conceptual representations and propositional attitudes (26). In a similar vein, Shadlen and Kiani claim that decision-making requires 'a commitment to a proposition or plan of action' and that 'it involves deliberation, planning, and strategizing' (2013, 791).

The assumption that anticipation or decision-making must involve such demanding cognitive machinery fuels accusations of anthropomorphism against those who defend plants cognition. Yet, we may ask why these capacities should be defined so narrowly. Huang et al. (2021), for example, argue convincingly that not all decisions (including some made by humans) involve deliberation or strategizing. The same may hold for anticipation (Stepp and Turvey 2010).

In our view, both Adams (2018) and Shadlen and Kiani (2013) risk committing *anthropofabulation* too. Anthropofabulation occurs when criteria for a cognitive capacity are inflated to match the most elaborate forms of human performance, and then applied as standards for other species (Buckner 2013). Even if adult humans typically deploy explicit beliefs and desires in the form of propositional attitudes and concepts, we can question whether those capacities extend to infants or many non-human species. As Segundo-Ortin and Calvo (2019, 69) warn, tying cognition too tightly to conceptual representation risks disregarding the complex behaviours observed across both the animal and plant kingdoms, unjustifiably narrowing cognitive science to human cases alone (J. Lee et al. 2023).

4.3 | Confirmation Bias

Cognitive biases can distort research in plant cognition research. One of the most familiar is confirmation bias (Nickerson 1998): the tendency to seek and privilege evidence that supports a working hypothesis while undervaluing contrary data. This bias threatens every stage of the scientific process, from hypothesis formulation and experiment design to data collection, analysis and interpretation.

Researchers in plant cognition may unintentionally design studies that favour their preferred hypotheses, for example by choosing methods likely to yield supportive results, or by highlighting patterns consistent with their views while overlooking alternative explanations. Neglecting control conditions that could rule out rival hypotheses also risks skewing interpretations and conclusions (Loehle 1987).

In phytoacoustics, selective hypothesis testing can lead to premature conclusions about sound perception in plants. Acoustic emissions caused by xylem cavitation, for instance, are primarily physical events: ruptures of water columns in the xylem that generate vibrations detectable as sound waves (Nardini et al. 2024). Caution is therefore needed before inferring that plants 'communicate' through sound. Although plant-emitted sounds may play some role in ecological interactions, the field is still nascent, and it remains an open empirical question whether these emissions are functional signals for communication (Calvo and Segundo-Ortin 2023).

A similar caution applies to research on common mycorrhizal networks (CMNs), the so-called 'wood-wide-web' (Beiler et al. 2010; Giovannetti et al. 2006). These underground fungal–root symbioses do facilitate the transfer of nutrients and water between tree roots and fungi, but their ecological significance is debated. For example, whether CMNs substantially benefit shaded seedlings remains unclear (cf. Simard 2018). Plants may exchange chemical signals through CMNs, but interpretations may be inflated by positive citation bias (Karst et al. 2023; Henriksson et al. 2023). Key uncertainties remain, though: how widespread CMNs are in natural forests, whether mature trees preferentially channel resources to kin, and to what extent greenhouse findings extrapolate to field conditions. Alternative explanations, such as improved seedling growth through direct soil nutrient transfer rather than CMNs, have either been neglected altogether or inadequately tested.

5 | Conclusion

The study of plant cognition raises fundamental questions about what counts as cognition and how it can be investigated in aneural organisms. In this article we have outlined the main theoretical frameworks—from computationalist and representationalist models to radical embodied and behaviour-first approaches—and considered how they might be integrated. We have also surveyed key methodological strategies, highlighting the value of comparative psychology and the role of philosophy in clarifying concepts, shaping experiments and guarding against epistemic pitfalls. Finally, we have examined the conceptual and practical challenges that confront this emerging field, including replicability concerns, anthropomorphism and anthropocentrism and confirmation bias.

Together, these discussions provide a conceptual and methodological foundation for plant cognition research. They underscore that progress depends on theoretical pluralism, rigorous experimental design, and openness to revising assumptions about what cognition entails. The companion article, **Plant Cognition—An Empirical Primer**, develops the other half of this project. It reviews the current state of empirical evidence—ranging from plant movement and decision-making to neurobiology and phytoacoustics—and considers the philosophical and ethical implications of these findings. Taken together, the two primers aim to provide a comprehensive guide to the conceptual, methodological and empirical landscape of plant cognition.

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