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Plant sentience revisited: Sifting through the thicket of perspectives

Author's Response on [Segundo-Ortin & Calvo](#) on *Plant Sentience*

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Abstract: In our target article (Segundo-Ortin & Calvo 2023), we proposed the intriguing possibility of plant sentience, drawing parallels with non-human animal studies. This response aims to sift through the rich thicket of perspectives offered by our commentators. To do so, we assess the risks of employing double standards, as well as the tendencies of anthropomorphizing and zoomorphizing in plant studies. We also emphasize the need for clarity in linguistic and conceptual terms, examine the neurophysiological evidence for plant sentience, and discuss the ethical implications of such recognition.



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1. Introduction.

Our target article (**Segundo-Ortin & Calvo**) invited the scientific community to investigate the possibility of sentience in plants, paralleling the studies conducted on non-human animals. Our argument is based on the surprising cognitive abilities plants exhibit and the potential for unique electrophysiological mechanisms of sentience distinct from those in animals.

We have been privileged to receive a wealth of commentaries in response to our target article, each offering unique insights and perspectives. Whereas the more sympathetic ones (e.g., **Henning & Mittelbach**, and **Rouleau & Levin**) provide further evidence that acknowledges the possibility of plant sentience, the more dismissive ones reject the idea upfront (e.g., **Mallatt et al.**, and **Robinson et al.**, both of whom critically examine the claims of plant sentience and find them unsupported by evidence). Commentaries further pick on: the distinction between sentience and cognition (and sensing) (**Bennett; Damasio & Damasio; Dung; Gutfreund; Robinson et al.; Struik; and ten Cate**); the alleged neurophysiological evidence, or lack thereof (**Broom; Dołęga et al.; Pessoa; Robinson et al.; Rouleau & Levin; Yilmaz**); the need for linguistic and conceptual

clarifications (**Booth; Brooks Pribac; Correia-Caeiro & Liebal; Ivanchei et al.**); the value and role of comparative analyses (**Birch; Henning and Mittelbach; Pessoa**), with a focus on the scientific underpinnings of plant and animal sentience, drawing comparisons and highlighting differences; the philosophical underpinnings of the debate (**Burgos & Castañeda; Carls-Diamante; Harnad; Plebe; Solé; Vallverdú**), contemplating the broader ramifications of recognizing sentience in plants; the overall empirical evidence and the directions for future research (**Dung; ten Cate; Baciadonna et al.; Henning & Mittelbach; Mallatt et al.; Mastinu; Tiffin**); and the foreseen ethical implications (**Baciadonna et al.; Milburn**), among others.

Given the overlapping themes and multifaceted angles presented, we have chosen to structure our Response thematically rather than by author. This approach allows us to address common threads holistically, minimizing redundancy. Additionally, we have quoted specific excerpts from our commentators at length, where appropriate, to ensure that we reflect their claims as accurately as possible and provide context to the general reader.

We are grateful to all the commentators for their invaluable engagement and contributions, and very much hope we are able not just to clarify but also to enrich the ongoing debate in a constructive manner. We would like to extend our special thanks to Stevan **Harnad**, both as the editor of *Animal Sentience* and as a commentator on our article. His insights, particularly his suggestion to introduce “a few terminological and conceptual distinctions,” have been invaluable in clarifying the discourse on sentience, especially in the context of plant sentience. We deeply appreciate his conducting role in facilitating this exchange and ensuring that it was both enlightening and productive.

In what follows, we will begin by exploring in section 2 the critical issue of potential double standards in animal/plant research on sentience. Section 3 tackles the nuanced topics of anthropomorphism and zoomorphism. Sections 4 through 6 are dedicated to clarifying key linguistic and conceptual terminologies, while also exploring redefinitions and disanalogies in this context. Section 7 provides an examination of the contentious neurophysiological evidence, or the notable absence thereof, pertaining to plant sentience. In section 8, we engage in the discussion about the potential markers that could indicate sentience in plants. Finally, section 9 shifts focus to the ethical implications arising from the concept of plant sentience.

2. The risk of introducing double standards.

As we note in our target article, the challenge of studying non-human sentience lies in the absence of direct evidence. This is why researchers must resort to indirect indicators, such as behavioural markers or electrochemical activity, to make inferences about potential conscious experiences. Aware that the difficulties of this reasoning by analogy increase when the subject of study (plants, in this case) is phylogenetically distinct from humans, we nonetheless observe a prevailing zoocentric bias in the study of sentience, which in our view needs rectification.

Bennett claims that although the empirical evidence suggests that there is something “akin” to plant cognition, “no amount of evidence for cognitive abilities in plants equates to evidence for plant sentience.” The reasoning of **Bennett** is:

“cognition would not be positive evidence for plant sentience in itself, and indeed, no amount of evidence for plant cognition would ever be evidence for sentience, *which is something fundamentally different.*”

We agree with **Bennett** that cognition and sentience should not be equated, with the proviso that, by the same token, no amount of evidence for cognitive abilities in *animals* equates to evidence for animal sentience, and that animal sentience is not required to understand or interpret the behaviour of animals in their environment. Reasoning otherwise, we hold, is to adopt double standards.

Bennett seems to employ such a double standard when claiming that our line of reasoning is weak. He insists that we

“do not present any evidence for the existence of plant sentience *per se*, only speculation based on incompletely understood phenomena.”

However, we must emphasize: we are not aware of any evidence in the animal literature that proves the existence of *animal* sentience *per se*. This is precisely why science must turn to indicators or markers (e.g., Crump et al., 2022), all of them indirect by necessity.

The “incompletely understood phenomena” that **Bennett** refers to concern anesthetics. He cites our target article to highlight perceived weaknesses in our argumentation:

“It is possible that anesthetics not only disrupt plant behavior but shut down plant sentience or awareness altogether” (**Segundo-Ortin & Calvo**).

It might be informative to revisit Crump et al.’s (2022) use of analgesia as a criterion for sentience:

“The animal’s behavioural response to a noxious stimulus is modulated by chemical compounds affecting the nervous system in [the following way]: Putative local anaesthetics, analgesics (such as opioids), anxiolytics or antidepressants modify an animal’s responses to threatened or actual noxious stimuli in a way *consistent with* the hypothesis that these compounds attenuate the experience of pain, distress or harm” [Crump et al. (2022); our emphasis].

Following this line of reasoning, it seems unlikely that **Bennett** would agree that this serves as evidence of animal sentience *per se*. In fact, when using this as an indicator or marker of animal sentience, all we could infer is that it's *possible* that anesthetics not only disrupt animal behavior but also shut down animal sentience or awareness altogether. This is precisely what we claim; and it is the reason we insist that more research is needed. In this sense, our position is compatible with the remark by **Dołęga, Siekierski & Cleeremans** that:

“this kind of intervention lacks the selectivity that is needed to distinguish between targeting the mechanism(s) responsible for sentience and disrupting all behavioral and cognitive capacities.”

The effect of anaesthetics in plants does not prove by itself that plants are sentient, but we can reason analogously, as in the animal sentience literature, that it can be an *indicator* of sentience, among others.

Other commentators fail to adequately acknowledge the inferential step involved when the experimental subject is an animal rather than a plant. **Damasio & Damasio**, for example, write that we wrongly conclude:

“that because general anesthesia in humans causes a radical loss of sensing that inevitably entails loss of consciousness, the response to general anesthetics in plants would also signify a loss of consciousness”.

However, it is important to note that we introduced this as a hypothesis, and never defended it as an assumption. Since we are not making this assumption, we don't need to defend it.

Adding to the issue of the double standard, **Bennett** also tells us that:

“The idea of sentience is hard enough to define in humans, let alone animals, and certainly impossible in the context of plants. But even if we could define what plant sentience would amount to, we can never know whether plants have it.”

But why, if we may ask, is it “hard enough” to define in non-human animals, yet “impossible” in plants? What determines that for some other-than-human organisms it can be defined, while for others, it *cannot*? **Bennett's** commentary does not provide an argument for that conclusion. He does, however, appeal to cultural factors, and concludes that:

“even if we could define what plant sentience would amount to, we can never know whether plants have it.”

However, we do not see why the same conclusion is not drawn for non-human animals. If animal sentience were clearly defined, could we ever truly know if animals possess it? We struggle to understand the inconsistency or lack of neutrality in the epistemic approach required to address both questions.

For the record, we are not alone in complaining about the aforementioned double standard. In their commentary, **Rouleau & Levin** note that:

“there is a double standard: behavioural patterns associated with subjective experiences in humans are considered valid for inferring cognition in non-human animals but not in diverse other systems including plants.... cognitive functions, including sentience, can potentially be achieved by very different systems and their disparate substrates.”

As the reader may guess, we could not agree more with **Rouleau & Levin**.

3. On anthropomorphizing/zoomorphizing.

The observation is made by **Struik** that:

“[a]ttributing sentience to plants reflects an anthropomorphic view of plants.”

Struik is not alone in highlighting the risk of anthropomorphizing (or more generally, of ‘zoomorphizing’) plants. Consider, for example, the complaint of **Robinson et al.** that:

“the humanization of plant life, or, more correctly, the application to plants of terms from mammalian sensory physiology (seeing, hearing, feeling, consciousness, intentionality), has no solid scientific basis. It perpetuates an anthropomorphic bias and misleads the uninformed reader.”

In a similar vein, **Carls-Diamante** warns us that the risk of anthropomorphizing is:

“an ever-present one in the study of plant cognition, perhaps even greater than in the study of animal cognition.”

Finally, **ten Cate** writes that:

“[d]espite S-O & C's statement that we should ‘be cautious and critical with metaphors and analogies’ it is hard to avoid the impression that they themselves regard the terms they use as more than metaphors describing the outcome of a process in anthropomorphic terms.”

We find the accusation of anthropomorphism puzzling. What is the basis for this charge? Unless we assume that sentience is a capacity that belongs only to human beings, we fail to see how considering the possibility that plants have felt states reflects an anthropomorphic view of plants. Nowadays, more and more non-human animal species are being considered sentient (and probably rightly so!) and none of these conclusions are regarded as anthropomorphic. By the same token, we do not see why the hypothesis of plant sentience implies this bias.

The charge of zoocentrism is a long-standing one. It sometimes concerns the methods being used to investigate plant behavior. For instance, in the past, some of our commentators have insisted that time-lapsing plants (one of the most valuable tools in studying plant behaviour) serves “to make them look more animal-like” (Taiz et al., 2019, p. 684).

The criticism that the use of time-lapse videos zoomorphizes plants is misplaced. Time-lapse techniques are not used to make plants appear “more animal-like” but to uncover intricate patterns in plant behavior that might otherwise go unnoticed to the naked eye (Calvo and Trewavas, 2020). These methods provide valuable data on various aspects of plant movement.

Regarding this last point, **Plebe** has highlighted the importance of time scale for debates about cognition and sentience. According to **Plebe**:

“[t]he challenge presented by the difference in timescales between plants and animals has been acknowledged by both proponents (Reber & Baluška, 2021) and critics (Mallatt et al., 2021) of the hypothesis that plants are sentient. However, this issue has primarily been framed as a difficulty in applying animal-based models to plants, rather than as a cultural barrier to accepting the notion of plant sentience.”

We hold that time-lapse is a useful way to overcome the barrier imposed by the differences in time scale in which phenomena occur in plants and animals, making us able to appreciate plant behavior. As we see it, it's not the techniques that are inherently zoomorphic; rather, the bias lies in how some choose to interpret them. We firmly believe that the biases they point out are more a reflection of their own perspectives than ours. In fact, a similar conclusion is drawn by **Tiffin**:

“It is worth noting, however, that, with a few exceptions, the bases on which some commentators address the target article seem rather anthropo/zoocentric and occasionally anthropo/zoomorphic (e.g., **Robinson et al.**).”

Moreover, **Plebe**'s notion of “constructive anthropomorphism” is worth considering. According to him, constructive anthropomorphism:

“can offer valuable heuristics in the early stages of research, providing a temporary vocabulary and analogies useful in planning experiments and gaining understanding [...]. Anthropomorphism is certainly a tool that must be handled with care. The differences in timescale may confer some useful constraints on our imaginations. In extending the vocabulary of psychological and neural states from humans to plants, the timescale disparity would force us to keep in mind how profoundly different sentience would have to be, if it existed at all.”

We welcome **Plebe**'s effort at reconciling scientific endeavors with common sense beliefs, acknowledging the valuable effort in directing the discussion about plant sentience toward a scientific path. If anything, our efforts in the past have been geared towards understanding how to customize experimental protocols imported from the animal literature for use in plant research, avoiding the risk of anthropomorphizing plants in the

process (for a detailed discussion of some of the hurdles in customizing animal protocols, see Ponkshe et al., 2023).

It is likely that none of this will move **Mallatt et al.**, who insist that:

“S&C also seem to sidestep the burden of proof by labeling their opponents “zoocentric,” meaning unwilling to consider that organisms other than animals may be sentient (pp. 1-2). No, the opponents are not close-minded or myopic, but are just declining to accept, without strong evidence, the extraordinary claim that plant sentience is produced by some unknown, hypothetical mechanism that does not involve a nervous system. It is now incumbent on plant neurobiologists to accept unequivocally that the burden of proof lies squarely on their shoulders.”

Mallatt et al. insist further that “[t]he road from romance cannot reach science while denying the burden of proof.”

We must reiterate that we *do* acknowledge the burden of proof and understand the need for stronger evidence. However, the sole method we're aware of for gathering such evidence and ensuring a robust data pool is through experimentation. These experiments must be tailored specifically because our subjects are plants, not animals, and spatiotemporal scales are crucial. To dismiss the project as doomed from the start is to overlook the fundamental issue and accept the *null* hypothesis from the onset. For us, the question of whether one taxon or another possesses sentience is a factual matter (*pace* **Gutfreund**; see section 8 below), and it's up to science to provide the answer. Is the current evidence sufficiently robust? Certainly not, and we are aware of this. But does that imply that efforts to gather data, which could either refute or confirm the hypothesis that non-neural life forms might be sentient are in vain? We trust that the rest of this Response to commentators clearly outlines our proposed approach.

We must call attention, however, to some claims made by our commentators that suggest that they are indeed being zoocentric, despite what **Mallat et al.** claim. For instance, **Mastinu** argues that a crucial difference regarding plants and animals is that the latter would actively seek for anaesthetics:

“A laboratory rat *consciously pulls* the lever to get its dose of narcotic. This aspect is absent in the plant kingdom.”

For **Mastinu**, this is a strong indicator that rats are sentient. Needless to say, **Mastinu** is right that plants do not pull levers to get anesthetized. However, we must note a crucial and problematic assumption in the argument: that plants must behave as animals for the hypothesis of plant sentience to be taken seriously. By imposing this requirement, we hold, **Mastinu** is asking us to judge plant sentience using animal standards. As with sentience, this is a strong indicator of zoocentrism.

4. Some words about words (and definitions): the case of “sentience.”

It cannot be dismissed that in some cases we might be talking past each other. A few words about *words* is thus in order. Since our target article is about sentience, it is with this notion that we choose to begin.

In our paper, we define sentience quite modestly as the capacity of an organism to feel, or to have felt states. We also claim that such feelings can include sensory experiences, be they external or internal. We thought that this definition was clear enough, but some of the commentators think otherwise. For instance, **Booth** tells us that:

“[t]he word ‘feel’ is ambiguous between the broad categories of sensation and affect [...] A ‘feeling’ might be both sensation and affect (such as in feeling comfortably or uncomfortably hot or cold), but the two should not be conflated.” [see also **Harnad**]

We agree with **Booth**, and this is why we decided to leave affect out of our initial (and, again, quite modest) definition of sentience. Hence, we are surprised by the remark of **Brooks Pribac** that by applying the term sentience to plants:

“the important distinction between affectively neutral sentient states and affectively valenced ones [**Milburn** see also **Booth**, and **Harnad**] is likely to get lost.”

Mastinu seems to agree with this remark. According to him, the evidence reviewed in our paper does not speak up for plant sentience, because:

“[it]is not sufficient to establish that plants can “feel” pain or pleasure or be otherwise aware of their behavioral responses.”

To repeat: we agree that sensation and affect are not the same, and, in fact, we find it likely that sentience is not a unitary, all-encompassing property but that different species have different sensory capacities, depending on their specific needs and their evolutionary history. In other words, there are probably a diversity of ‘sentience profiles’ in the natural kingdom, with species being able to feel some basic states (heat, cold, drought), and others being able to feel comfort, discomfort, pain, and so on, on top of the former. What sorts of feelings plants have, if any, is a matter of empirical research, as **Carls-Diamante** rightly points out. We also agree with **Milburn** that only some of these felt states have ethical significance and, if discovered in plants, would force us to rethink our relationship to plants (more on this in Section 9).

Another alleged source of confusion, this time highlighted by **Damasio & Damasio**, is between “sensing” and “sentience”, who write:

“[t]he hypothesis that plants might be sentient confuses the notion of sentience (or consciousness) with that of sensing.”

We are deeply puzzled by this assertion. First of all, since **Damasio & Damasio** do not cite any specific passage from our target article where we conflate the two, we must conclude that the misinterpretation lies in their reading of our stance. Second, it is evident that sensing and sentience are distinct concepts, and we must underscore that any indication of an organism's sentience is, at best, an indirect “informed guess”. We all agree about this, we believe. But it is important to note that this is equally true for animals and for plants. This leaves us wondering why **Damasio & Damasio** state that the hypothesis of plant sentience *in particular* conflates sensing with sentience. If the evidence for sentience is always indirect, why is it the case that *only* the hypothesis of plant sentience is making the aforementioned confusion? Note, again, the risk of introducing double standards.

Broom nonetheless disagrees with our (and many others’) position that non-human sentience cannot be directly observed. According to **Broom**:

“[t]housands of scientific papers contradict this [...] according to the view of S&C, it would seem that no certain evidence about the mental state of any animal, including any human, can ever exist.”

Broom concludes that, if our position is right, then the project of investigating other-than-human sentience is doomed. We do not think that this project is doomed. Quite the contrary. We shall let **Rouleau & Levin** respond in our behalf, if we may, since, as they correctly point out:

“cognitive scientists have become increasingly willing to attribute sentience to members of the animal kingdom despite our longstanding inability to measure subjective experience directly in any species (including humans). Indeed, all attributions of cognition (i.e., mental actions), including sentience, are always inferred on the basis of embodied behaviours, including verbal self-report in humans. If felt states in humans and other animals are always inferred, why is the same leap from observable behaviour to inferred sentience not afforded to other organisms, including plants?”

For us, this question is critical, but the inferential leap appears to take different forms depending on the kingdom under consideration, unfortunately. According to **Damasio & Damasio**:

“[sentience] opens [an] organism to the possibility of deliberate behavior. Deliberate behaviors are available in humans, obviously, but also, we presume, in numerous species equipped with a nervous system and sentience. We expect all mammals, birds, reptiles, and fish, to be sentient/conscious and we venture that so are some insects.”

Setting aside the circular nature of **Damasio & Damasio**'s argument that sentience:

“opens the *sentient* organism to the possibility of deliberate behavior. Deliberate behaviors are available in humans, obviously, but also, we presume, in numerous species equipped with a nervous system and *sentience*.”),

we fail to see why all mammals, birds, reptiles, and fish are automatically considered sentient, while for insects, it's only a possibility. We do not necessarily disagree with **Damasio & Damasio**; we merely observe that they do not clarify their reasoning or specify the evidence guiding their distinctions.

Building on our earlier remarks, it is evident that positioning ourselves as the infallible gold standard carries significant risks, a stance we have already underscored. And yet **Ivanchei et al.** resort to such a gold standard too when they claim that:

“higher-order theories of consciousness require the existence of unconscious representations alongside conscious ones.”

In arming their theoretical argument, they consider Global workspace theory (Baars, 1988; Dehaene & Changeux, 2011) and the theory of higher-order thought (Brown et al., 2019). carries significant risks, a stance we have already underscored. And yet **Ivanchei et al.** state:

“[b]ased on the consciousness literature, we develop an argument that to ascribe sentience to a system one needs to show both conscious and unconscious manifestations of the system. This view is based on a theoretical and a methodological argument. Given that potential criteria for sentience were primarily developed in the human consciousness literature, we will use that literature to establish the argument.”

On the theoretical front, we first diverge from **Ivanchei et al.**'s human-centric perspective. In our previous work (Segundo-Ortin & Calvo, 2021), we examined various theories of consciousness, both reductionist and non-reductionist—the former seeking to pinpoint biophysical mechanisms and material substrates, and the latter aiming to discern the type of non-mechanistic principles that might underpin sentience as an emergent phenomenon.

Reductionist approaches include the Cellular Basis of Consciousness (Reber 2018; Reber et al., 2023), Information Integration Theory (Tononi et al., 2016), and Quantum-based approaches (Hameroff 1998; Barlow 2015). Non-reductive approaches encompass Predictive Processing theories based on the free-energy principle (Friston 2010; Calvo &

Friston 2017), as well as ecological (Chemero 2009) and enactive (O'Regan 2014) theories of consciousness.

Despite their evident diversity in terms of function and structure, these theories share the assumption that sentience likely did not emerge *de novo* in humans or within the animal kingdom. The evolutionary plausibility of theories of consciousness has brought to prominence the concept of plant sentience. Thus, irrespective of the degree of credibility given to any particular theory, be it reductionist or non-reductionist, it is evident—contrary to **Ivanchei et al.**—that Global Workspace Theory and the theory of higher-order thought do not represent the entirety of theoretical possibilities.

Moving on to their methodological argument, **Ivanchei et al.** encourage us:

“to demonstrate plant sentience empirically begin by developing a workable dissociation paradigm.”

In **Ivanchei et al.**'s view:

“[a] possible application in the plant context might be to try to contrast processing of external stimuli that have local effects in a plant to processing that leads to a larger coherent movement of a plant.”

We are thankful for **Ivanchei et al.**'s constructive feedback and are eager to accept the challenge. However, two caveats are warranted. First, we must incorporate a variety of frameworks in this endeavor, as indicated in our previous comment. Second, it is important to recognize that “finding dissociable signatures of conscious and unconscious processing” does not necessarily mean that the effects are behavioral. Conscious and unconscious processing might “produce different or even opposite behavioral effects”, as well as other types of non-behavioral (e.g., electrophysiological) effects.

Assuming that we are open to theoretical frameworks beyond Global Workspace Theory and the theory of higher-order thought, we might discover that if consciousness correlates with, say, the degree of information integration, an electrophysiological approach could be used to study this integration in plants. To summarize, as Mediano et al. (2021) have elucidated,

“if plant consciousness depended on the capacity of the vascular system to support complex patterns of electrical activity distributed among interacting bundles of vascular tissue (i.e. integrated) whilst being information-rich, the vasculature of higher plants may well fit the bill.” [Mediano et al. (2021)]

5. On the definition of cognition.

Interestingly, a number of commentators pick on the idea that cognition and sentience are to be told apart. For the record, we agree with this distinction, as demonstrated by the fact that we introduce a series of cognitive markers as *possible indicators* of sentience.

Some authors disagree with our use of ‘cognition’ though. For instance, **ten Cate (2023)** notes that we break away from the allegedly well-agreed definition of cognition introduced by Shettleworth, according to which:

“cognition refers to the mechanisms by which animals acquire, process, store, and act on information provided by the environment” [Shettleworth (2010)].

According to **ten Cate** we attribute cognitive capacities to plants (such as decision-making, anticipation, and the like) but that we:

“shift the definition of cognition away from the causal one [...] i.e., away from what proximate processes and mechanisms underlie a particular behavior, to its consequences”.

What this seems to imply is that cognition refers to a series of mechanisms that underlie and thus make it possible that organisms can make decisions, anticipate future contingencies, learn by association, etc. And, since we do not provide any information about such mechanisms, we have not found cognition in plants. Even worse, according to **ten Cate**, this is something well-agreed in the field. Similarly, **Booth** criticizes our use of terms such as 'feelings', 'behavior', 'cognition', and 'sentience', accusing us of employing them “without reference to scientific criteria established by experimental psychology.” According to **Booth**, both cognition and sentience resort to “transforming informational content between input and output.” Plants, **Booth** suggests, are neither cognitive nor sentient, because they do not perform such input-output transformations.

There are different things worth considering here. First, that plants do not transform informational content between input and output is debatable. In fact, paraphrasing Adamatzky et al. (2017), **Vallverdú** claims that:

“plants can provide a reliable way to design computational systems. It might be possible to combine them with computation following engineering principles because of their intrinsic mechanistic properties.”

Leaving aside the disagreement between **Booth** and **Vallverdú** about plant computation, a second point deserves consideration. It is simply not true that cognition is a well-defined term used to denote a series of specific mechanisms or processes that must be realized by all organisms to be called cognitive. If anything, the evolution of cognitive science has shown us that 'information-processing' is a misleading concept, and what we have in the field is a sort of explanatory pluralism, with more and more cognitive scientists convinced that the same cognitive functions could be made possible by different mechanisms or processes (Allen, 2017). In fact, an analysis of introductory textbooks on psychology and cognitive science reveals a lack of uniform definitions. For example, Amsel (1989) highlighted this ambiguity long ago when the founding editor of the journal *Cognitive Psychology* humorously stated that cognition is “What I like.”

Note, too, the risk of begging the question here. Suppose that plants are able to perform some of the behaviors we call cognitive in other species, but they do so by other means (means that are not computational). Would it be reasonable to conclude that plants are not cognitive? Would it not be more fruitful to take the case of plants as a starting point for a comparative analysis of cognition? After all, if we do not define vision *causally*, restricting it to that of species with chambered eyes, there is no reason to do it with cognition. As Segundo-Ortin and Calvo (2018) noted, by positing specific input-output transforming mechanisms as the *hallmark* of cognition, we run the risk of imposing important and undue limitations to our comparative cognition, leaving out of consideration *a priori* many forms of sophisticated behavior displayed by plant and animal species.

That many researchers happen to resort to their preferred definition of cognition does not mean that that definition is either the one and only one, or the most appropriate one. In fact, a coarse reading of the set of commentaries suggests that what we all mean by “cognition” is far from settled. For example, **Yilmaz** writes that:

“One can think of “cognition” as a basic capacity of all organisms, including single cell organisms such as *E. coli* (van Duijn et al. 2006). Organisms have evolved various kinds of cognitive capacities through evolutionary processes, and plants have their own ways of cognizing.”

We fully agree. Elsewhere, we have explored a broader understanding of cognition from an embodied and biological perspectives, according to which cognition is fundamentally a biological function aimed at interacting beneficially with the environment. (Calvo and Keijzer, 2011; Segundo-Ortin and Calvo, 2019). Within this framework, cognition is understood in terms of perception-action interactions, extending beyond just human-level thinking to encompass a broader spectrum of phenomena. Cognition would be realized by different mechanisms that make it possible that organisms navigate and adapt to their environment, bridging the gap between basic biological processes like metabolism and more complex behaviors.

Concluding from our discussions, we are not asserting that ours is the definitive or sole perspective on cognition. Rather, we wish to emphasize that it is an oversimplification and misrepresentation of the diverse landscape of cognitive sciences to presume that the community uniformly adheres to Shettleworth’s definition. That is, after all, just one among many conceptualizations and does not have any inherent or privileged status over other interpretations. As in all scientific inquiries, it’s essential to approach these definitions with an open mind, appreciating the richness of thought and nuance that has gone into formulating them. Our own approach is in fact the opposite: let’s agree on the behaviors we want to call “cognitive” regardless of the species, and then look for the mechanisms that make these cognitive behaviors possible. Like **Rouleau & Levin**, we favour a “system-agnostic approach” to cognition and sentience, one that does not presuppose anything about the means of cognition.

It is important to point out that we are not equating the hypothesized cognitive abilities of plants with mere adaptations either. Some of our previous experimental research at MINT Lab suggest that the presence of a pole affects the nutation patterns of common bean shoots (Raja et al., 2020). By way of commentary, **ten Cate** writes:

“[u]sing adaptiveness as criterion for calling a process cognitive hence does not make much sense: it is hard to imagine the evolution (and persistence) of a cognitive mechanism that is not adaptive... [a]s in the case of the vine behavior, other examples presented of the plant’s responses to certain environmental triggers also seem to be labelled as ‘cognitive’ mainly because they are beneficial, adaptive.”

ten Cate disagrees with our definition of cognition, **Mallatt et al.** notes, because:

“[a]lthough his own definition does not demand a brain or mental processes, it requires a consideration of the causal mechanisms behind behaviors, which S&C’s definition leaves out. Instead, S&C only consider adaptive responses. Merely being adaptive is not a criterion for the presence of cognitive or sentient processes.”

We agree that behaviours should be not only adaptive but also sufficiently flexible, proactive, and goal-directed (Calvo & Lawrence, 2023; Segundo-Ortin & Calvo, 2019, 2021). These are by no means a definitive set of necessary and sufficient conditions for a behaviour to be considered cognitive. However, they can sometimes help distinguish the purely adaptive from the genuinely cognitive. We fail to see why this commits us to a false dichotomy, as **Mallatt et al.** contend. In their view, we:

“posit a false dichotomy by acknowledging only two possible explanations of plant behavior, hence if one is wrong the other must be right. According to S&C, plant behavior is either (1) hardwired, mechanical, and inflexible (in their mischaracterization of the traditional view),

or (2) sentient, volitional, cognitive, and intelligent. But there is a third, intermediate, possibility—that plant behavior is flexible and complex but does not involve sentience.”

We cannot see how our presentation of the different cognitive behaviors of plants could induce such a reading. We repeat several times in the target article that cognition, *by itself*, does not imply sentience. It follows from this distinction that plants could be cognitive (not automata) without being sentient.

Perhaps it is more interesting to come back to the objection that we are overlooking the causal mechanisms behind plant behaviours. Contrary to **Mallatt et al.**'s suggestion, our approach in the bean study does not overlook the causal mechanisms behind behaviours; it simply addresses *one* aspect of the problem. In Raja et al. (2020), we wrote:

“our research introduced a cutting-edge methodology to study the dynamics of plant nutation movements. Unlike traditional kinematic analyses focused on shape, period, or amplitude, our approach centred on three distinct aspects that are widely recognized in the biological and behavioural dynamics literature as signatures of adaptively controlled processes and motions when found in other organisms: harmonicity, predictability, and complexity.” [In Raja et al. (2020)]

In theory, this methodology can be applied to a broad spectrum of movements, including plant movements. Does this imply that a dynamical analysis provides a comprehensive explanation? Certainly not. The causal mechanisms governing the nutational behaviours of common beans remain to be identified. This underscores the need for further research inquiries. Referring to the aforementioned study by Raja and colleagues (2020), **ten Cate** argues that:

“[e]xplaining the complexity of the vine’s behavior in terms of ‘*controlled ... to attain a ... goal*’ S-O & C attribute purposeful foresight to the vine, thereby taking this to be indicative of the presence of sentience.”

For **ten Cate**, our description of the empirical finding of Raja et al. in terms of endogenous control incurs in “teleological reasoning.”

The first thing to note is that the language of “endogenous control” is not ours. Rather, Raja et al. claim that:

“a mechanism that is not merely influenced by endogenous factors, and that is sensitive to the position of a support to climb the environment of the plant, proves to be a better candidate [to explain the behavior of the vine]” [Raja et al. 2020]

Is this language just a metaphor? It is important to remember that Raja and colleagues have taken:

“three typical signatures of adaptively controlled processes and motions, as reported in the biological and behavioral dynamics literature: harmonicity, predictability, and complexity.” [Raja et al. 2020]

When applied to human and non-human animals, these signatures are assumed to be present in behaviours that are goal-directed and endogenously controlled. Now, if **ten Cate** is right that we must regard this language as metaphorical, then we must do so for animals and plants alike. It is difficult to see how we can use some terms for some cases and not for others if we are observing the same phenomena in all of them. Once again, **Rouleau & Levin** express this view in a clear and crisp way:

“If behaviour is the window to sentience, evaluation criteria must focus on observable response patterns without reference to the means by which they are produced.”

This is exactly what Raja et al. did: we stuck to the observable behaviour.

6. More on (re)definitions and (dis)analogies.

In comparative cognition, there is a risk that key concepts are used in rather idiosyncratic ways. This has been stressed by **Mallatt et al.**, who charge us with:

“redefin[ing] standard neuropsychological terms, giving them unfamiliar meanings that fit plant behaviors.”

The same is argued concerning some cognitive capacities, such as decision-making. **Mallatt et al.** note:

“Decision-making, in standard definitions, involves minds and mental pondering: ‘making up one’s mind as to an opinion, course of action, etc.’ (Oxford English Dictionary). But S&C use the following redefinition of Reid et al. (2015) that does not require a mind as a central controller: ‘the action by an entity (individual organism or group) of selecting an option from a set of alternatives, based on characteristics of the alternatives that the entity can perceive’.”

Again, as with "cognition", **Mallatt et al.**'s criticism assumes that there is a universally accepted definition. We hope we all agree that, regardless of the direction of the debate, the Oxford English Dictionary is not the appropriate reference to resolve the matter. Elsewhere we have discussed plant decision-making at length (Lee et al., 2023). Recent studies suggest that even non-neural organisms, like bacteria, exhibit decision-making abilities, as indicated by markers that are commonly accepted in the human and non-human animal literature. In this literature, decision-making is typically understood as the process of choosing between multiple behavioral options based on the information gathered. Evidence from bacterial behaviour, particularly *E. coli*, shows that they can switch behaviors adaptively, on the basis of environmental cues, a process that mirrors decision-making in more complex organisms. These bacteria utilize distributed control systems to evaluate and respond to their environment without a centralized system.

Control systems do not always follow a hierarchical pattern (where mechanisms are arranged in ascending levels of control); instead, they are sometimes arranged heterarchically, meaning that they can operate somewhat independently without a centralized governing body, gathering, processing, and acting on information about the internal and external states of the organism. Contrary to what is commonly believed, current neurophysiological evidence indicates that mammalian brains realize this heterarchical organization as well, and that many sophisticated human decisions could result from heterarchical neural control systems (for a detailed analysis, see Bechtel & Bich, 2021; Huang et al., 2021). This decentralized approach challenges **Mallatt et al.**'s traditional view that decision-making requires a central executive mechanism.

In apparent agreement with **Mallatt et al.** that the way we use concepts is problematic and somewhat pseudoscientific, **Struik** writes:

“definitions and concepts that are commonly used in work on human cognition and sentience are stretched to make them broad enough to also include plant phenomena. [...] The case is then built from there, mainly from indirect and weak evidence (or no evidence at all), speculating mainly from further analogy [...] The result is that there is a set of slightly distorted definitions and concepts that together create a new reality, its main advantage being to provide room for new hypotheses and innovative ways of thinking.”

A case in point, according to **Struik**, is the term ‘behaviour,’ which he considers inappropriate for plants. Importantly, whereas the idea of ‘plant behaviour’ has faced

skepticism in the past (Lee et al., 2023), 'behaviour' can be defined in ways that include plants:

“the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes” (Levitis et al., 2009, p. 103).

This definition of behaviour, which avoids referencing movement, does not exclude plants or sessile organisms. On the contrary, the crucial aspect is the internal coordination and control of actions by the organism, irrespective of any locomotion (see Cvrčková et al., 2016).

This said, we wonder why extending the notion of behavior beyond mere locomotion is a pseudoscientific move; the reasoning behind this charge is not apparent. We think the generalization is justified and potentially fruitful for comparative psychology. Thinking of locomotion as *one* type of behavior, and putting the stress on the capacity of organisms to control their responses to environmental conditions, can raise scientifically productive questions concerning, for example, the multiple realizability of the same functions stressed by so many of the commentators on Key (2016). (Multiple realizability will be further XXXXX later in this Response.)

Another conceptual dispute is highlighted by **Correia-Caeiro & Liebal**, who argue that to claim that plants communicate with other plants when releasing VOCs we should be able to demonstrate “that plants releasing VOCs intended to inform other plants.” In fairness, **Correia-Caeiro & Liebal** remain open to the investigation of purported plant communication, regardless of the similarities and differences to animal communication. As **Correia-Caeiro & Li** point out,

“to infer first-order intentionality, S&C would need evidence that plants have control over the production of VOCs and are releasing them with a communicative goal... Do plants show any of the evidence of intentionality [...]? For example, do plants release more VOCs if other plants are in close proximity (i.e., do they show “audience effects”)? [...] Does VOC-production change if there is wind in the direction opposite to the intended “receiver” plants (i.e., sensitivity to social partner ability to receive signal)? [...] This tilts against their conclusion: “plants seem to have zero-order intentionality (which excludes communication).”

We acknowledge the challenges in this area and accept **Correia-Caeiro & Liebal's** viewpoint. The emerging field of 'plant bioacoustics' suggests that sounds emitted by plants may play a role in regulating plant-ecosystem interactions to some extent. However, this field is still in its infancy (Demey et al., 2023; Hussain et al., 2023; Khait et al., 2023; Waqas et al., 2023); as it continues to expand, the majority of the findings have yet to be independently replicated. Many questions remain open and unanswered at the time of this writing.

At this stage, we do indeed have more questions than answers; for this reason, we are grateful to **Correia-Caeiro & Liebal** for highlighting these critical issues. What we currently understand is that certain stressors, such as drought, cutting, or viral infections, may trigger the release of ultrasonic sounds that carry information (Khait et al., 2023). The emerging insights in plant bioacoustics suggest that some sounds could play a role in initiating defensive strategies. Other research is exploring the concept of directional, phonotropic responses—reactions to sounds that carry significant ecological value, such as the sound of water. Buzz pollination represents yet another burgeoning area of study.

It is evident that many sounds produced by plants, such as those resulting from 'cavitation'—the formation of air bubbles in the xylem that emit noise as they move through or burst within vascular tissues—are involuntary (Waqas et al., 2023). However, there is also speculation that plants may emit voluntary sounds for communicative purposes, such as the acoustic inhibition of non-kin plant growth (Demey et al., 2023). At this juncture, caution is imperative. We agree that many questions about plant sounds remain to be explored, but a body of evidence is gradually accumulating in support of these theories. Numerous urgent inquiries persist, from the ecological significance of plant sounds to the mechanisms responsible for producing these purported voluntary emissions. Is sound a medium for bidirectional interaction among plants? (Demey et al., 2023; Hussain et al., 2023; Khait et al., 2023). The answer remains elusive.

The distinction between involuntary and voluntary sound emissions can be linked to observations made by **Mastinu**, who notes that:

“[t]he plant is not “conscious” of emitting molecules. When we approach an automatic door, it opens. We “communicate” to the door to open; it opens with an automatic response. Mancuso and colleagues have observed that radical tips can orient their growth to specific sound vibrations that can be traced to water (Gagliano et al. 2017; Rodrigo-Moreno et al. 2017; Mancuso & Baluska 2018; Calvo et al. 2020). Sound waves (not soil moisture) determine the orientation of the root toward the source of the sound. Again, is this a matter of cognition? Or perhaps an automatic response?”

It is indeed conceivable that plant responses are not fundamentally more complex than an automatic door, where a sensor activates a mechanism to automatically open or close the door. In fact, Adams (2018) has made this comparison before to suggest that plant behaviors are informationally driven but not cognitive. However, using the automatic door as an analogy may oversimplify the actions of plants by comparing them to rudimentary reactions. Unlike garage doors, which react to single cues, plant interactions with their environment are almost never triggered by isolated signals. As we have discussed elsewhere, plants respond not only to magnitudes and directions of environmental variables, but also to their temporal dimensions, as well as the relations they have to other variables. This, we hold, “is anything but unsophisticated ‘garage door’ behavior” (Segundo-Ortin & Calvo, 2019, p. 66).

Finally, we would like to comment on **Mallat et al.**’s emphasis on the pivotal role that the principle of parsimony has in guiding our scientific inquiries. We agree that parsimony is useful when selecting between competing theories or paradigms. Yet, it stands alongside other values such as empirical accuracy, consistency, broad scope, and fruitfulness (Kuhn, 1977). Although there are instances where we might lean towards simpler theories, the simplest theory is not always the true one. Opting for a particular paradigm encompasses a multifaceted interplay of these values, historical context, and the subjective judgments of the scientific community. The annals of science offer numerous examples to ponder (but we need not don our Philosophy of Science hat at this juncture).

Instead, to briefly divert our attention to more trivial matters, we hope the editor-in-chief overseeing these exchanges, **Harnad**, will permit us, despite not being native English speakers, to point out a lexical oversight in **Mallat et al.**’s commentary. The term “imparsimony” does not exist in the English language—or at least, it is not found in

standard dictionaries¹. Given that our commentators have dedicated significant attention to dictionary definitions, we trust they'll take this observation in jest as we near the midpoint of our Response. Now, back to the core discussion.

In their section titled "Imparsimony," **Mallatt et al.** contend that:

"[a]ssuming that sentience is a highly complex phenomenon arising from complex physical processes (Mallatt & Feinberg, 2021), we reason that if a behavior can be explained more simply by known physiological or biochemical processes, then that behavior does not rely on sentience. Simplest explanations are preferred. This is the parsimony principle that guides scientific inquiry. The proponents of plant sentience fail to apply it."

We must admit that we're somewhat perplexed. Are **Mallatt et al.** suggesting that as soon as human physiological and biochemical processes are completely understood, human behavior will no longer depend on sentience? Does this mean that as we gain more scientific insights into the physiological/biochemical foundations of human behavior, there will be less justification for recognizing human-level sentience? We find that hard to believe; and, naturally, we presume **Mallatt et al.** do not intend to suggest such a corollary. However, if that's the case, their argument remains elusive to us.

7. On neurophysiological (lack of) evidence.

We explore next the discussions about the lack of a central nervous system in plants and its implications for plant sentience. In doing so we address the comparisons made between plant signaling systems and animal neural structures. In section 3 of our target article, we reviewed electrophysiological processes that might underpin, if only in part, plant cognition and sentience. We ended that section with general remarks about the implications of our findings. As we noted, while it may be premature to attribute sentience to plants (given the lack of consensus on the required biological features) dismissing plant sentience solely because plants lack a centralized brain or neurons is based on an assumption and begs the very question we are trying to address. Yet, several commentators continue to focus on the functional neurobiology of consciousness and the absence of a central nervous system in plants. We will try to clarify our position further.

Broom contends that plants "lack a central nervous system, which is a prerequisite for sentience." He further elaborates in his commentary referencing a previous publication of his (Broom, 1998), where he *defines* a feeling as

"a brain construct involving at least perceptual awareness which is associated with a life regulating system, is recognisable by the individual when it recurs and may change behaviour or act as a reinforcer in learning."

We think that to define feelings according to a brain construct is to beg the question. We suggest simply removing the word "brain" and defining a feeling as a construct. Period. But **Broom** insists:

"a nervous system with some degree of brain development is required in order to have an experience."

Of greater concern, **Broom** notes that there are many parallels between plant and animal cells but insists that:

¹ "imparsimonious" exists and is in use; "imparsimony" is hence an eligible nominalization, and is itself [occasionally used](#). Not every esoteric lexicalized or lexicalizable [variant](#) is in the lexicon. -ed.

“none of the examples [advanced in our target article] indicate that there is a nervous system in any plant.”

Such claims are perplexing, as we were clear that plants do not have a nervous system.

We did note, however, that the reported similarities between the nervous system of animals and the non-neural vascular system of higher plants have motivated some researchers to broaden the definition of a nervous system. Note, in addition, that this line of inquiry is in the interest of making functional comparisons between physiological structures, and of promoting “a better understanding of how evolution has driven the features of signal generation, transmission and processing in multicellular beings” (Miguel-Tomé & Llinás, 2021, p. 1). This functional angle, we suggest, may be the source of the misunderstanding and M-T & L’s opposition to the term “plant neurobiology.” To be clear, we are not very interested in terminological disputes. We think these disputes may obscure the many molecular-level similarities found between animal and plant signaling systems, and the possibility that these similarities may underpin the same cognitive functions we appreciate at the level of the organism.

Dołęga et al. shift the focus from the purported necessity of a nervous system and suggest that:

“demonstrating plant sentience would require that we identify not only behaviors analogous to those exhibited by sentient creatures, but also the functional analogues of the mechanisms causing such behaviors.”

The same claim is advanced by **Carls-Diamante** who insists that we seek higher functional analogies between the internal signaling systems of plants and animals. We wholeheartedly concur with this suggestion. Indeed, this is why our target article’s title includes a question mark and why we insist on the need to promote the scientific inquiry on the topic.

A number of commentators take a more sympathetic approach to our views. **Pessoa** welcomes our “call for a rigorous science of plant behavior and physiology.” Advancing a distinction between anatomical and functional centralization (the latter not needing to be implemented in terms of the former), **Pessoa** writes that:

“with processing through interactions of many spatially distributed areas rather than a master ‘controller’.”

Pessoa goes on to write that “certain forms of functional centralization might still be important”, as exemplified by the integrated way in which compact bodies move around.

We agree with the heterarchical approach endorsed by **Pessoa**. As we observed in the target article and reiterate here (see section 6, above), Bechtel and co-authors have argued that:

“many decisions in nature, including some performed by mammals and human beings, are controlled by heterarchically distributed mechanisms” [**Segundo-Ortin & Calvo**, p. 7].

These mechanisms act as control systems which make local decisions based on particular information parameters, allowing organisms to stay alive in complex environments. Surely, plants use control systems to measure and assess environmental factors based on survival standards too; controls that are not top-down but can operate independently without a central “boss.” Rather than an oversimplification of the way plants (or bacteria, the preferred example) make their choices, non-hierarchic/centralized ‘executive’ mechanisms serve to emphasize specific, widespread control systems that still gauge and interpret environmental cues in a flexible manner.

In line with the aforementioned remarks, we agree with **Rouleau & Levin** when they claim, based on the concepts of ‘multiple realizability’ and ‘substrate independence’, that:

“if different organizations of nervous tissue can achieve the same functions, the possibility that cognitive capacities, including sentience, can be achieved by other tissues should be considered.”

These concepts clearly apply to hierarchically vs. ‘heterarchichally structured’ control systems. As **Rouleau & Levin** observe:

“It is highly implausible that all sentient life in the universe achieves felt states using the neural circuitry underlying human consciousness on earth. Plant sentience is likely to be the tip of the iceberg of sentient systems yet unknown.”

Robinson et al. further discuss the comparison between the plant vascular system and the animal nervous system. Their position starkly contrasts with that of **Rouleau & Levin**. For instance, **Robinson et al.** write that many of the neurobiological properties we claim to be shared by animals and plants “demand clarification, if not refutation.” Specifically, they refer to: (i) “plant neurotransmitters” and anesthetics; and (ii) signaling in plants and its purported resemblance to neural transmission. In what follows, we will try to clarify our position on both fronts.

Regarding (i), **Robinson et al.** turn to Wikipedia for a definition of ‘neurotransmitter.’ This definition stresses the necessity of a neuron secreting a signaling molecule to affect another cell across a synapse. They claim that the most common neurotransmitters are glutamate, gamma-aminobutyric acid (GABA) and acetylcholine, and that the former two do act as signaling molecules for plants. However, based on their preferred definition, they conclude, that they “do not fit the definition of neurotransmitters because plants lack synapses (Robinson & Draguhn, 2021)”.

As we see it, placing unwavering trust in Wikipedia, or even dictionary definitions, is a risky venture. Take, for instance, the *Oxford Dictionary*'s definition of “action potential”: “The change in voltage that occurs across the membrane of a nerve or muscle cell when a nerve impulse is triggered.” Or consider the definition from *Encyclopaedia Britannica*: “the brief (about one-thousandth of a second) reversal of electric polarization of the membrane of a nerve cell (neuron) or muscle cell.” Given these descriptions, should we deduce that action potentials do not occur in plants simply because these definitions do not accommodate the type of action potentials generated by cells other than neurons or muscles? Clearly not. Electrical propagation in plants entails direct cellular connections through plasmodesmata and conductive vascular bundles of fibre. This direct coupling obviates the need for synapses. This is no revelation to **Robinson et al.** They're undoubtedly aware, more so than we are, that plant cells can also produce action potentials. So, what's the takeaway regarding dictionary definitions, especially when some are seemingly biased towards synapse-centric discussions? Either we treat these definitions with the reverence they command, or we do not—but consistency is key.

The crux of the matter is that specific compounds, recognized as neurotransmitters and neuromodulators in animals, also contribute to electrical signaling in plants. This holds especially for substances like GABA and glutamate. In plants, these compounds disperse in ways reminiscent of the diffusion patterns of neuromodulators in animal systems. As underscored by Miguel-Tomé & Llinás (2021), citing Toyota et al. (2018), glutamate's presence can catalyze a surge in calcium ion concentrations, facilitating electrical signal transmission in plants, particularly post-injury. Current plant research is rethinking GABA, viewing it not just as a metabolic offshoot but also as a pivotal signaling compound

(Bouché et al., 2003; Bouché & Fromm, 2004). The multifunctionality of these molecules in plant processes, from growth to stress responses (Žárský, 2015; Ramesh et al., 2017), sheds light on the evolutionary progression of neurotransmitters. Some researchers contend that GABA signaling pathways might be an evolutionary staple (Bouché et al., 2003), while others ponder the ubiquity of glutamate receptors, hinting at potential evolutionary links between fundamental metabolism and cellular communication in multicellular entities (Žárský, 2015).

With regard to anaesthetics, **Robinson et al.** wonder whether the way volatile anesthetics affect plants indicate plant sentience. They reason that:

“[the] similarities are too sparse to support the hypothesis [...] that plants are sentient organisms merely because they lose responsiveness under anesthesia.”

As explained elsewhere (Lee and Calvo, 2023), the exploration of anaesthesia in plants provides potentially vital insights into the primary effects of anaesthetics across various species. The successful application of anaesthesia to plants demonstrates the universal significance of electrical signaling principles and their interruption across diverse biological realms. One conceivable theory suggests that, as in animals, anaesthesia hinders the transmission of action potentials (APs). Anaesthesia affects GABA and glutamate, both crucial for the generation of APs. The profound capability of anaesthetics to halt motor responses in animals, plants, and protists has been noted (Baluška & Mancuso, 2009a; 2009b), with the responsiveness to anaesthetics probably evolving in unicellular organisms as “an adaptation to boundary membrane homeostasis and ion channels activities to changing environmental conditions” (*ibid.*, p. 62). This perspective hints at the potential existence of inherent anaesthetic-like compounds in plants, with ethylene being a notable example. Further research into these plant-derived anaesthetic analogs is certainly merited but, as noted in Lee & Calvo (2023), when we separate anesthetic mechanisms from neural pathways, similarities become evident across various organisms. Such a spectrum encompasses entities “from paramecium to primate” (Kelz and Mashour, 2019). The ramifications of this are significant, going beyond mere ion channel operations or the impact of anesthesia on mitochondria and the cytoskeleton (Jakšová et al., 2021). Studies on the influence of anesthetics on both flora and fauna, we suggest, may hint at a broader underlying principle.

Let’s now turn to **Robinson et al.**’s second point—(ii) signaling in plants and its alleged similarity to neural transmission. Here, they address both action potentials (APs) and slow wave potentials (SWPs). We begin by considering APs.

Robinson et al. contend that “there is no “electrochemical equivalency” between plants and animals.” In support of their claim, they consider:

“the fact that the electrochemical origin of APs in nerves is completely different from that in plants, involving a Ca^{2+} influx rather than a Na^+ influx” [and] that “the propagation of plant APs is 100 to 1000 times slower and, unlike neuronal APs, is associated with a wave of elevated cytosolic Ca^{2+} .”

In insisting on the lack of an “electrochemical equivalency” we run the risk of overlooking possible functional equivalences. Of course, these equivalences need to be found empirically for the case of plant sentience, but it is good to have in mind the possibility that sentience is multiply realizable, as **Rouleau & Levin** note.

We do acknowledge that numerous distinctions exist between plant and neuronal APs. Lee and Calvo (2023) delineate five primary differences, grouped into two categories:

variations in molecular components and variations in electrical and signaling properties within and between cells. Specifically, the differences encompass: (i) the molecular components responsible for depolarization; (ii) the dynamics of the falling phase and hyperpolarization, and differences in the electrical and signaling properties within and between cells, such as (iii) the average resting potential of plant cell membranes compared to that of neuronal cells; (iv) the rate of propagation, wherein the relative slowness of plant action potential propagation is probably due to the characteristics of the phloem. These characteristics include a higher activation threshold for chloride channels, a sparser density of ion channels, differences in inherent activation kinetics, the necessity for signals to cross cell-to-cell junctions, and the lack of myelination as observed in nerves (Hedrich and Neher, 2018; cited in Lee and Calvo, 2023); and (v) varied durations of the refractory period.

Despite the differences, the essential *functional* characteristics distinguishing APs from other electrical potentials remain intact. As underscored by Lee & Calvo:

“[plant APs] “are induced by voltage depolarisation, follow an all-or-nothing principle, possess a threshold potential, and travel at constant velocity and amplitude (Zawadzki et al. 1991). They also follow the three-fold structure of neuronal APs. Moreover, plant APs exhibit absolute and relative refractory periods post-firing.” [Lee and Calvo (2023)]

To cut a long story short, plant and animal action potentials are functionally similar in that they both serve as rapid, reliable means of electrical signal transmission. They follow similar patterns of initiation, propagation, and termination, ensuring effective communication and response to stimuli. The question, as **Sidney-Diamante (2023)** and **Dołęga et al. (2023)** rightly point out, is whether these functional similarities are relevant to sentience. This is part of the research we want to pursue.

We also understand that beyond observing similarities in APs across plants and other organisms, and utilizing plants as study subjects, it's crucial to acknowledge their distinct features. Plants uniquely employ APs for communication between subterranean and surface structures and for interactions with other plants and fungi. In the realm of plant electrophysiology, there are unique electric potential types, including 'local electrical potentials' (LEPs), 'variational' or 'slow wave potentials' (VPs or SWPs), and 'system potentials' (SPs). LEPs, although generated locally, are integral to plant physiology.

SWPs, activated by damage, traverse the plant but differ notably from APs. They produce varying signal magnitudes (deviating from the all-or-none principle), move at reduced speeds, are regulated by fluid pressure, and are transmitted through the xylem. Interestingly, SWPs seem to trigger APs. Meanwhile, SPs are extensive hyperpolarization events—the opposite of depolarization—that can, for example, travel from one leaf to another. To grasp the essence of plant APs, it is imperative to view them in the context of a more intricate and unique electrical signaling framework.

Robinson et al. devote an extensive subsection to slow wave potentials and wounding, following their brief discourse on action potentials. We genuinely appreciate their informative overview of SWPs and have attentively considered the details. **Robinson et al.** conclude that:

“wound-induced signaling in plants is therefore a complex form of electrical communication unique to plants” [and that this] “is in no way comparable to the transmission of electrical signals in neurons.”

We agree. However, our stance never relied on equating plant wound-induced electrical signaling with neuronal electric signals.

Consider, too, the insights offered by **Solé**. His commentary encourages us to take a step back and broaden our perspective, transitioning from the intricacies of electrical potentials to the topologies of biological networks. In particular, **Solé** considers:

“two crucial features of ‘solid’ brains” [...] “(1) intermediate elements that allow information processing beyond the sensor-effector metaphor [and] (2) re-entrant loops, might be a critical requirement for sentience.”

Solé then poses the question whether there is something in plants that we can map onto any of these topological features. In his view:

“in plants the dynamics are limited to single leaves, with no integration beyond this scale.”

We appreciate **Solé**'s thoughtful contributions. Indeed, the concept of re-entrant structures in plants has been broached, albeit largely as a theoretical proposition. It has been posited that anastomoses and plasmodesmata might serve as foundational elements within a network of vascular cells, enabling the creation of intricate topologies and potentially establishing the re-entrant ‘dynamic core’ (Mediano et al., 2021).

We cannot understand, however, why **Solé** affirms that:

“the dynamics are limited to single leaves, with no integration beyond this scale.”

An extensive literature highlights the many ways plants integrate information systemically beyond the scale of single leaves (Cahill et al., 2010; Costa et al., 2023; de Kroon et al., 2009; Huber & Bauerle, 2016; Kong et al., 2018; Moulton et al., 2020; Novoplansky 2016; 2019; Reid et al., 2015; Souza et al., 2017). **Solé** might accordingly rethink his stance with respect to the position of plants in the “cognitive (morpho)space.”

8. Markers of sentience.

To set the stage for our exploration of potential markers or indicators of sentience, as suggested in the animal literature, it is useful to first address certain preliminary criticisms.

Gutfreund argues that, rather than scientific, questions about sentience are cultural, and therefore the scientific quest for sentience is doomed, regardless of whether the focus of our research is plants or animals. The reasoning behind **Gutfreund**'s view is that:

“the scientific method is limited and agnostic about the question of the distribution of consciousness, in any system, including plants and animals.”

Gutfreund opens his commentary with an alleged case of a *reductio ad absurdum* (RAA) by Integrated Information Theory (IIT), a controversial theory of consciousness (Fleming et al., 2023). Moving all the way from this alleged instance of a RAA to our target article, **Gutfreund** writes:

“[not] only does the target article fail to provide convincing evidence to support plant sentience, but it raises questions, analogous to RAA, about the validity of the ways we define and measure consciousness in other species.”

We disagree with **Gutfreund** on two counts: (1) The argument he considers to be RAA is not. (2) His view on the divide between science and culture is ill-founded. Consider first his *reductio* of IIT.

RAA is a form of argument where, starting from some premise or assumption, one shows that this assumption leads to an absurd conclusion. The goal is to demonstrate that the original assumption is untenable, and therefore, that the opposite must be true.

According to **Gutfreund**, IIT is an example of RAA. His claim is that the assumptions of the theory lead to the "clearly ridiculous" conclusion that the internet is conscious. He then asserts that this conclusion serves as a refutation of IIT via RAA. However, simply claiming that some conclusion is absurd is insufficient. One must demonstrate that the conclusion is absurd, showing for example, that the statement is contradictory. Since we do not defend IIT in our target article, we do not need to spend more time with this issue. We just want to note that much more work is needed to refute IIT the way **Gutfreund** aims to do.

More interesting is **Gutfreund**'s approach to science and culture:

"There is no experiment or observation to distinguish who is right and who is wrong; we cannot even say who is more likely to be right. In this respect, the target article fails to move the debate over plant sentience from romanticism to the realm of science."

Gutfreund places significant emphasis on a Popperian falsificationist methodology and the epistemic value of parsimony. Yet, his discourse suggests a somewhat reductive understanding of the complexities involved in applying the scientific method. The issue with sentience, **Gutfreund** believes, is that

"the only reason we talk about it is that we feel it and it is important for us. Apart from our subjective feelings, consciousness is not part of scientific theory... consciousness in scientific theories of behaviour is neither parsimonious nor falsifiable; scientists are expected to remove such unnecessary elements from their theories."

We find these comments concerning the explanation of observable phenomena in science rather perplexing. Take, for instance, black holes, electrons, or even dark matter. Surely, the use of the term "observable" in relation to entities like subatomic particles demands some elucidation. In the commonplace understanding—directly perceiving something with our eyes—electrons have not been "observed." Yet, in experimental physics, "observation" typically refers to detecting the impacts or traces of an entity, rather than directly visualizing it. Electrons, though not directly observed, can be inferred through indirect means (see Bird, 2023 for a recent analysis of the role of observation in science).

Observations of the electron typically involve gauging probabilities and interactions rather than "seeing" it in a conventional sense. The existence of electrons gives rise to an *inference to the best explanation*, but not merely on the basis of adhering to Popperian methodologies. It is unclear to us why sentience should not be explored in a similar vein, even if it cannot be directly observed. After all, **Gutfreund** seems certain that cognitive behaviors are observable, as he states that:

"Physical, chemical, biological, ecological and evolutionary theories explain observable behaviours, cognitive and non-cognitive alike."

We struggle to comprehend why the debate on cognition (including plant cognition) is firmly within the realm of science, yet the discourse on sentience cannot possibly be. In both cases, we are inferring the presence of cognitive and sentient states from observable traces in the behavior of an organism.

Of a different nature is the critique of **Birch**, who is a firm defendant of the principle that sentience can be studied scientifically. **Birch** compares developmental plasticity in plants and animals, aiming to “[disentangle] sentience from developmental plasticity”. We are in fully accord with this. Keeping the two apart is necessary regardless of the biological kingdom in question. **Birch** nonetheless concludes that the notion that plants make decisions must be metaphorical:

“Watching a bean shoot develop in time-lapse is fascinating and spectacular. Likewise, there is remarkable developmental plasticity in animals, and watching any animal embryo develop in time-lapse is fascinating and spectacular. It is an astonishing feat of chemical and bioelectric signalling, coordination, and differential gene expression [...] It is very natural to talk metaphorically of an animal or plant making ‘decisions’ or ‘choices’” as it develops.”

Birch resorts to reasoning by analogy to support his conclusion:

“Animal development is not normally guided by conscious choice [...] So, the path to seeing plasticity as evidence of sentience requires us to set aside one of the most basic, most fundamental pieces of common ground in animal sentience research. We are being asked to take seriously the possibility that, while sentience has no role in guiding development in animals, sentience in plants does have this role.”

Three points are worth considering here:

(1) The first point is the assumption that decisions must be inherently conscious. This claim contrasts with many approaches to decision-making in psychology and the cognitive sciences, which include non-conscious decisions as legitimate decisions. Huang et al. (2021), for example, have made a convincing case that not all decisions (including decisions made by human beings) are conscious.

(2) The second point is the analogy between developmental plasticity in animals and in plants. For **Birch**, the comparison is enough to make the idea that plants are sentient problematic: **Birch** believes that just as we do not consider developmental plasticity in animals to be guided by sentience, we should not consider it to be so in plants. We think this is an oversimplification. Plant and animal development differ drastically from one another. Although plant development begins with embryogenesis, unlike animal development, it is, in plants, a postembryonic, indeterminate and ongoing process. Apical meristematic tissues, through cell division and enlargement, continuously give rise to organs in adulthood throughout the vegetative phase of the life cycle of the plant (Taiz & Zeigber, 2010). Plant development is in this way extremely plastic, with light—along with many other environmental parameters (Calvo & Trewavas, 2020)—allowing adult plants to adapt their patterns of growth and development to a wide range of conditions. Such developmental patterns exhibit markers of endogenous control and goal-directedness (Raja et al., 2019). Perhaps, as **Birch** argues, the developmental plasticity of plants is not guided by sentience, but comparing it with the developmental plasticity of animals misses some crucial differences.

(3) The third point is the reduction of plasticity in plants to developmental plasticity. The commentary by **Henning & Mittelbach** may prove useful here. It elaborates on a previous study (Mittelbach et al., 2019) reporting an intricate system of rewards and pollen distribution. (Some plants appear to adapt their pollen presentation by modulating stamen movements based on learned visitation patterns.) **Henning & Mittelbach** discuss the evolution of plant behavior, using the *Loasaceae* family as an example. Mittelbach et al. had observed a progression in the complexity of floral behavior across different species, driven by interactions with pollinators. They suggest that this

behaviour involves controlled stamen movement. Crucially, their findings underscore that plants exhibit not just phenotypic plasticity, but behavioral plasticity as well. They interpret this as challenging the traditional distinction between plants and animals in terms of behavior and sentience.

We now turn to other facets of **Birch**'s analysis, especially his comparison between plants and invertebrates. Having addressed the "neuro" aspect in a previous section, we now turn our attention to the other distinction **Birch** highlights.

Invertebrate research, in contrast to plant research, is not based on speculation. On the contrary, in studying invertebrates, **Birch** writes:

"[one] can directly apply experimental approaches used to assess pain in mammals, such as conditioned place preference tests, and observe behaviour that, if the animal were a mammal, these tests would clearly indicate pain... This leads to a challenge for plant sentience researchers: if you can demonstrate conditioned place preference akin to that seen in octopuses, many of us will have our confidence shaken... It is hard to tell whether [**Segundo-Ortin & Calvo**] see the evidence they cite as raising the probability of sentience. In my view, it does not. I think (i) it is fair to be initially very sceptical of the idea of plant sentience, and (ii) evidence obtained so far has not given us grounds to revise the probability upwards, but (iii) careful attempts to obtain new evidence are welcome. I hope that **Segundo-Ortin & Calvo**, in their responses, can state whether they agree. If they disagree, I hope they can state which parts they disagree with."

We are happy to take up the gauntlet. Not necessarily because we are certain about demonstrating, say, conditioned responses in plants, but simply because we are curious to find out. As of now, there is no need to compromise any conviction (that plants lack sentience), given that the evidence is still inconclusive.

It's now time to explore the markers or indicators themselves. **Dung** consolidates recent research on markers that are often cited as compelling evidence for animal sentience (references from Sneddon et al., 2014; Birch et al., 2020; Dung, 2022; Crump et al., 2022; and Dung & Newen, 2023). Should plants meet (some of) these criteria, they could also start to be deemed sentient. In our target article, **Dung** highlights two such potential indicators: (1) that plants seem to engage in complex decision-making processes, integrating and weighting information from different states and context-dependent trade-offs to give priority to some responses over others; and (2) that plants can learn by habituation and association.

Given that all five references address motivational trade-off behavior in non-human animals, **Dung** examines plant decision-making and risk sensitivity, and concludes that "there is evidence of similar kinds of trade-offs in plants." However, **Dung** focuses on studies where motivational trade-offs are combined with elements of memory, which in turn "increases the demand for information integration." As we have previously discussed decision-making, we will center our attention on memory and associative memory in this context.

Dung writes that he knows of:

"no evidence that trade-offs that rely on associative memory can be performed by *C. elegans*, let alone plants."

Loy (2021) provides an excellent review of experiments on invertebrates, plants, and unicellular organisms, suggesting evidence of associative learning among invertebrates. Still, we concur that there is insufficient proof for this in single-celled organisms and

plants. As we explained in our target, article we cannot report conclusive evidence for or against associative learning in plants either. Currently, we are trying to replicate independently Gagliano et al.'s (2016) experiments on learning by association. However, there are serious deficiencies in the Gagliano et al. study; a substantial number of methodological factors must be addressed prior to settling the issue (Ponkshe et al., 2023). Alongside the exact replication, we are attempting a conceptual replication (Crandall & Sherman, 2016) which addresses all these shortcomings.

Dung concludes:

“[i]f plants do not meet the criteria for attributing sentience to animals, it is hard to see how attributing sentience to plants can be justified.”

Again, we fully agree. That is why our target article, to reiterate, was titled “Plant sentience?” (note the question mark). And that is why our aim is to focus on doing the science. Do we have the empirical evidence that plants meet the criteria listed in Sneddon et al., 2014; Birch et al., 2020; Dung, 2022; Crump et al., 2022; and Dung and Newen, 2023? No, we don't. Do we want to pursue that line of research and find out which criteria plants might meet, if any? Yes, we do.

Dung urges us to move from “simple forms of learning, including some forms of classical conditioning, [that] do not require sentience” to more complex forms, such as trace conditioning. In trace conditioning, however, there is a gap without any stimulus between the CS and the US. Therefore, a subsequent ‘trace’ of the CS is necessary to connect the interval before it gets associated with the US.

Recent literature reports trace conditioning in *Drosophila* (Grover et al., 2022) and in honeybees and other insects (Paoli et al., 2023; Szyszka et al., 2023). **Dung** writes that:

“if findings of classical conditioning in plants could be replicated, this would not do much to support the view that plants are sentient.”

Again, we are happy to take up the gauntlet. Our aim is first to find out whether plants can learn by simple association; and if so, whether plants exhibit more sophisticated forms of conditioned responses, such as trace conditioning.

One way or another, we applaud **Dung's** observation that:

“[w]hen plants have a particular behavioral capacity, we often take that as evidence that that behavioral capacity does not require sentience, rather than as evidence that plants are sentient. This methodological issue would benefit from explicit discussion in the future.”

We have noticed skeptics taking the opposite *ad hoc* approach on numerous occasions in the past. That is not the case of **Baciadonna et al.** They flag the aforementioned “lack [of] essential controls or fail[ure] to produce replicable results” but they would agree with us insofar as:

“agnosticism about sentience should not deter us from investigating unexpected new capacities in plants.”

In fact, **Baciadonna et al.** conclude that although associative learning is yet to be proved in plants, the research is worth doing, this time with properly designed and replicable experiments. We appreciate their openness. This represents the constructive spirit of adversarial collaboration in science that we advocate.

Baciadonna et al. comment on both Gagliano et al.'s (2016) study and on the one conducted by Bhandawat et al. (2020) on aversive conditioning in *Arabidopsis thaliana*. Because we have already explained where we stand concerning the former study, we will

only comment on the latter. As **Baciadonna et al.** explain, Bhandawat et al.'s study, lacking key controls, does not support associative learning in *Arabidopsis*. We agree, but a proper study is going to take time. For one thing, and on top of the considerations that **Baciadonna et al.** mention, before inferring associative learning (classical conditioning), it is important to eliminate the possibility of pseudo-conditioning, something that Bhandawat et al.'s study does not control for, among other issues (thanks to Aditya Ponshe for helpful comments on the specifics of Bhandawat et al.'s study).

To conclude this section, we would like to consider the proposal advanced by **Burgos & Castañeda**. They present panpsychism as a wider framework within which to contemplate plant sentience, prompting us to reflect on panpsychism and its potential consequences. **Burgos & Castañeda** state:

“everything is sentient, not just animals and plants, but also viruses, bacteria, single cells, even inorganic objects like tables, chairs, hats, rocks, computers, and doorknobs.”

The proposition that sentience could be a universal attribute is a general philosophical stance. This an intriguing outlook, the focus of our target article was more specifically on plant life. We think that each entity, be it plant, animal, or electron, warrants an individual and thorough investigation to ascertain the existence or nonexistence of sentience. **Burgos & Castañeda** challenge us to consider Goff's “constructive panpsychism,” according to which:

“electron sentience is vastly simpler than plant sentience, which in turn is vastly simpler than rat sentience, etc. Simpler sentient entities combine to form more complex sentient entities.” [Goff (2017)]

Regrettably, we are unable to articulate our position on Goff's panpsychist theory, as we have not engaged with the 2017 Goff text (*Consciousness and Fundamental Reality*). A further question, however, is posed by **Burgos & Castañeda**:

“S&C would be likely to ask whether electrons display the behaviors they take as indicators of sentience. There is as yet no evidence for an affirmative answer, although there is some evidence of Pavlovian conditioning (which is one indicator of sentience for S&C, p. 10) in certain inorganic systems (e.g., Broer, 2020; Zeng et al., 2020; Zhang et al., 2020)”.

This is a fascinating observation; we welcome the opportunity to respond. We might indeed consider biomimetic inspiration, as suggested by **Burgos & Castañeda**, such as “a synthetic material that emulates algorithmically associative learning” (Zeng et al., 2020). However, there is a clear distinction between algorithm-based biomimetic inspiration and the actual discovery of Pavlovian-type conditioning in inorganic systems at the implementational level. To be clear, there is no *fundamental* barrier to science exploring associative learning in inorganic forms. Such an endeavor, however, would encounter limitations on two fronts:

(1) Not all forms of associative learning would qualify as indicators of sentience. We would need to identify 'enhanced forms of associative learning' (Birch et al., 2020), which serve as markers for sentience, such as Unlimited Associative Learning (UAL) or 'trace conditioning' that operates across temporal gaps (Crump et al., 2022).

(2) whereas future experiments might confirm the presence of Unlimited Associative Learning (UAL) and/or trace conditioning in various taxa/phyla (Linson et al., 2021) or even in inorganic systems, the latter would still need to adhere to standard experimental

controls. To put it simply, a robot equipped with a 'Pavlovian polymer' (Broer 2020) demonstrating a conditioned response would have to undergo a series of routine tests. Consequently, we would anticipate that in such polymer-based learning robots, the intensity of both the conditioned stimulus (CS) and the unconditioned stimulus (US) would correlate with the effectiveness of the training. Similarly, the effectiveness should increase with a shorter interval between these stimuli and a higher number of pairings. In the same vein, we would expect the conditioned response to weaken and eventually vanish when the stimuli are no longer paired, and for the conditioned response to be triggered by stimuli sufficiently similar to those used during training. If all these conditions were met in plants, it would provide solid evidence that associative learning has occurred (Abramson & Chicas-Mosier, 2016). The same criteria would apply to any other system, whether biological or artificial. Nevertheless, we maintain that this would merely be an initial step towards creating “actuators that algorithmically mimic *elementary* aspects of learning” (Zeng et al., 2020; emphasis added).

Somewhat related to these concerns, **Vallverdú's** approach to studying minimal cognition in entities such as slime molds may provide insight into more complex cognitive systems, whether natural, hybrid, or entirely artificial. We appreciate his insightful commentary on this potential intersection. The perspective on unconventional computing and the role of plants in this field is both fascinating and stimulating. Specifically, unconventional computing aims to bridge two main areas: (i) the application of engineering techniques to biological materials, and (ii) the reverse-engineering of biological systems to comprehend their complex information processing capabilities. We agree that this could lead to groundbreaking solutions and a more profound understanding of cognition across different entities. However, while unconventional computing methods are indeed inspired by biological processes, it is crucial to delineate how these methods are directly relevant to plant cognition. A more thorough examination of this relationship would solidify the case for plant-based computation. Elaborating further is nonetheless beyond the scope of this Response.

9. Ethical implications.

A number of commentators chose to discuss the ethical implications of plant sentience, in line with our observation that “the ethical implications for our treatment of plants will need to be considered too.” Special mention is required for **Milburn**, whose commentary is fully devoted to such implications. This is especially needed, considering that previous discussions have typically ignored taxa outside the animal kingdom. **Milburn** writes:

“Part of taking the possibility of plant sentience seriously is to ask what its ethical consequences would be.”

However, if plant sentience ultimately challenges veganism on ethical grounds, it would not alter any future evidence supporting plant sentience. The question of whether plants are sentient is independent of the complexities it may introduce and we must keep both issues separated. Echoing this concern, **Broom** suggests that:

“[plant sentience] is not only empirically incorrect but potentially harmful to the efforts to protect the welfare of sentient beings... the benefits of the concept of sentience would be eroded if it were used for too wide a range of organisms.”

We appreciate the discussions unfolding in many ethicist circles, and we do not want to hinder the efforts made by animal welfarists. However, we think it is important to remind the reader about the distinction (already introduced) between affectively neutral sentient states and affectively valenced ones, independently of the organism's kingdom of origin in the tree of life. In our view, the question of interest for ethicist should be whether there is any form of pain or stress inflicted upon the organism that eventually becomes our food, and if inflicting such harm is truly necessary. The possibility that plants may be able to feel some states does not necessarily mean that their sentience needs to be equated to that of other-than-human animals, for they may not be able to have affectively valenced felt states.

Furthermore, the question of whether a significant portion of living entities are sentient should not be determined based on the challenges it may pose. We think it is unjustified to refuse to consider seriously the possibility that plants may be sentient *only because* this may force us to rethink our way of living. One way or another, were plants to be sentient, **Tiffin** notes:

“the ethical problems raised are not insurmountable, and would not threaten the now proven case for animal sentience.”

We think it is unacceptable to reject the hypothesis of plant sentience before engaging in serious investigations because we are afraid of its potential ethical consequences.

We disagree, however, with the suggestion of **Mastinu** that:

“[s]entience would not add anything to the plant kingdom. The complexity and importance of photosynthetic organisms is independent of whether they are sentient.”

By that logic, should we conclude, *mutatis mutandis*, that the complexity and importance of non-photosynthetic, heterotrophic organisms, such as animals, are independent of their sentience? We struggle to understand why sentience would matter for one group and not the other. As **Struik** notes:

“[a]ssuming that plants are sentient might [make our moral responsibility and respect towards plants even more urgent, raising the question whether moral responsibility and respect should be accorded to them collectively, as a community, or also as individuals.”

Coining the expression “plant liberation” (see Calvo & Lawrence, 2023, chapter 8) raises the concern, for **Brooks Pribac**, that it:

“may attract members of the public who are genuinely concerned about the possibility of plant sentience and will use the information to perform a critical self-evaluation towards greater personal integrity—but mostly it will be used to fuel sensationalism, misinformation and moral laziness.”

Our antidote to sensationalism, misinformation, and moral laziness is education. The potential for misinterpretation on the part of many only underscores the need for enhanced pedagogical efforts, not a dismissal of plant sentience based on potential misconceptions about its implications. Philosophers and activists should take this job seriously, in our view.

We anticipate that future discussions will include ethical considerations related to plants, or at a minimum, that the insights herewith discussed will influence policies aimed at flora conservation. After all, caring for plants will ultimately be advantageous for everyone (Calvo & Lawrence, 2023).

10. Conclusion. Let us close by expressing our gratitude for the engagement and insights provided by all the commentators. We reiterate the importance of continued dialogue and research on the topic of plant sentience. As noted by **Tiffin**:

“[j]ust a few decades ago] it was thought inconceivable that insects were sentient. Yet continuing research in that field has tended firmly in the direction of recognizing insect sentience [...] [It] would be irrational to deny the possibility that future work [...] could someday prove that plants feel too.”

We agree that much more discussion is still needed before accepting the idea of plant sentience. However, this should not deter us in our pursuit of knowledge. In this sense, we concur with **Vallverdú** that:

“[i]t is important to explore such a new field of research despite the incompleteness of the empirical support for it.”

In essence, we disagree with those who flatly dismiss the potential for plant sentience for the reasons mentioned and join with **Yilmaz** in promoting collaborative research between plant and animal researchers. We hope this series of exchanges has not only clarified but also enriched the ongoing discussion by encouraging forward-thinking. If history teaches us anything about science, it's the value of boldness.

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